



ACTA
XX CONGRESSUS INTERNATIONALIS
ORNITHOLOGICI

CHRISTCHURCH, NEW ZEALAND
2-9 DECEMBER 1990

VOLUME I

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ACTA
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ORNITHOLOGICI

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2-9 DECEMBER 1990



20TH INTERNATIONAL ORNITHOLOGICAL CONGRESS LOGO

The distinctive logo for the Congress was designed early in 1986 by Karen Pinnel, a Wellington Polytechnic design student. As part of her third year course at the Design School she was asked to design a simple graphic using a native bird from New Zealand. The final graphic chosen by the New Zealand Organising Committee for its simplicity, style and eye-catching appeal is based on the endemic Yellow-eyed Penguin, but the slightly more golden crest colour is representative of the distinctive crested penguin species concentrated in the New Zealand region. The Organising Committee wishes to record its thanks to Karen for her donation of the copyright for the use of the design to the New Zealand Ornithological Congress Trust Board. With penguins only being found in the southern hemisphere this logo is representative of the 'Southern Perspective' theme for the 20th International Ornithological Congress.



'NEW ZEALAND 1990'

Coordinated and promoted by the New Zealand 1990 Commission, activities under this theme are designed to commemorate a milestone year in the nation's history. Some of these formal milestones are 1000 years of known habitation of New Zealand; 150 years of the founding of modern government, and the cities of Auckland and Wellington; 100 years of a one person one vote electoral system. Throughout 1990 the country is formally recognising and celebrating the achievements of past and present with a wide range of local and international functions and expositions. Participating events will encourage New Zealanders to highlight and celebrate their natural advantages; increase awareness, understanding and appreciation of all cultures in their society; promote harmony, goodwill and tolerance; increase opportunities for sharing and partnership; and encourage thinking about the future.

The 20th International Ornithological Congress is an integral part of New Zealand 1990. The New Zealand Ornithological Congress Trust Board is pleased to acknowledge the support and participation of the 1990 Commission in the Congress.

ACTA
XX CONGRESSUS INTERNATIONALIS
ORNITHOLOGICI

CHRISTCHURCH, NEW ZEALAND

2-9 DECEMBER 1990

VOLUME I

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PREFACE

These *Acta XX Congressus Internationalis Ornithologici* provide a full and representative record of the activities of the 20th Congress held in Christchurch, New Zealand, 2-9 December 1990. Following the tradition of some recent International Ornithological Congresses, the *Acta* include all symposia papers - as well as plenary papers and business reports. In a departure from tradition, we have included as a Supplement to the *Acta*, the Programme and Abstracts distributed at the Congress so as to more fully report the scientific content of the Congress. Most of the symposium papers presented are included in these Proceedings. An abstract is presented if a complete manuscript was not received by the due date.

We have sought to minimise the time lag between the Congress and the publication of its Proceedings. Authors of published papers were asked to follow strict editorial guidelines. Conveners of the 48 symposia agreed to take on the task of editing and refereeing papers in their symposia. The post-Congress editing of these *Acta* has thus been substantially reduced. To streamline production, most text was optically character read directly from the manuscript for typesetting. Proofs were not returned to authors for checking but were proof-read by the editors.

Our policy, advised to contributors when they were sent editorial guidelines, has been to reproduce papers in the form in which they were received, subject only to standardisation of typestyle and format during the typesetting process. In general, texts and figures are reproduced in the form the authors submitted them, although some tables have required resetting. If authors did not conform to the recommended style their papers were not changed, except where inconsistency within the paper was evident.

We thank conveners and authors for responding to our request to adhere to editorial guidelines and deadlines, and we particularly appreciate the assistance of Prof. Dr. Peter Berthold, Chairman of the Scientific Programme Committee, for negotiating with many conveners and authors on our behalf.

Ben D. Bell
Secretary-General
Convener, Editorial Subcommittee

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INTERNATIONAL ORNITHOLOGICAL CONGRESSES 1884 - 1990

No.	City	Year	President	Secretary-General
I	Vienna	1884	Dr G.F.R. Radde	Dr Gustav von Hayek
II	Budapest	1891	Prof. Victor Fatio, Otto Herman	-
III	Paris	1900	Dr Émile Oustalet	Jean de Claybrooke
IV	London	1905	R. Bowdler Sharpe	Dr E.J.O. Hartert J. Lewis Bonhote
V	Berlin	1910	Prof. Dr Anton Reichenow	Herman Schalow
VI	Copenhagen	1926	Dr E.J.O. Hartert	E. Lehn Schiøler
VII	Amsterdam	1930	Prof. Dr A.J.E. Lönnberg	Prof. Dr L.F. de Beaufort
VIII	Oxford	1934	Prof. Dr. Erwin Stresemann	Rev. F.C.R. Jourdain
IX	Rouen	1938	Prof. Alessandro Ghigi	Jean Delacour
X	Uppsala	1950	Dr Alexander Wetmore	Prof. Dr Sven Hörstadius
XI	Basel	1954	Sir Landsborough Thomson	Prof. Dr Adolf Portmann
XII	Helsinki	1958	Prof. J. Berlioz	Dr Lars von Haartman
XIII	Ithaca	1962	Prof. Ernst Mayr	Dr Charles G. Sibley
XIV	Oxford	1966	Dr David Lack	Prof. Dr N. Tinbergen
XV	Den Haag	1970	Prof. Dr Nikolaas Tinbergen 1966-1969 Prof. Dr Finn Salomonsen 1969-1970	Prof. Dr Karel H. Voous
XVI	Canberra	1974	Prof. Jean Dorst	Dr H.J. Frith
XVII	Berlin	1978	Prof. D.S. Farner	Rolf Nöhring
XVIII	Moscow	1982	Prof. Dr Lars von Haartman	Prof. Dr V. Ilyichev
XIX	Ottawa	1986	Prof. Dr Klaus Immelmann	Dr Henri Ouellet
XX	Christchurch	1990	Prof. Charles G. Sibley	Dr Ben D. Bell

Acta of Previous Congresses

- I.** Sitzungs-Protokolle des ersten Internationalen Ornithologen-Congresses, der vom 7. bis 11. April 1884 in Wien abgehalten wurde. Wien, Verlag des Ornithologischen Vereines in Wien, 1884. vi + [90] pp. Mitteilungen des Ornithologischen Vereins Wien, Band viii-x, 1884-86.
- II.** Bericht . . . Zweiter Internationaler Ornithologischer Congress, Budapest, 1892. (Blasius) [n.p.; 1891] 58 pp.
- III.** III^e Congrès Ornithologique International, Paris, 26-30 juin 1900. Compte rendu des séances publié par É. Oustalet . . . et J. de Claybrooke . . . Masson et Cie, Paris. xii + 503 pp. 1901. [= Ornithologia, vol. 11]
- IV.** Proceedings of the IVth International Ornithological Congress, London, June 1905. Edited by R.B. Sharpe, E.J.O. Hartert, J.L. Bonhote. Dulau & Co., London. 696 pp. 1907. [= Ornithologia, vol. 14]
- V.** Verhandlungen des V. Internationaler Ornithologen-Kongresses, Berlin, 30. Mai bis 4. Juni 1910. Herausgegeben von Herman Schalow . . . Deutsche Ornithologische Gesellschaft, Berlin. x + 1186 pp. 1911.
- VI.** Verhandlungen des VI. Internationalen Ornithologen-Kongresses in Kopenhagen, 1926. Herausgegeben von Dr. F. Steinbacher. Berlin. vi + 641 pp. 1929.
- VII.** Proceedings of the VIIth International Ornithological Congress at Amsterdam. Amsterdam. vii + 527 pp. 1931.
- VIII.** Proceedings of the VIIIth International Ornithological Congress, Oxford, July 1934. Edited by F.C.R. Jourdain. Oxford University Press, Oxford. x + 761 pp. 1938.
- IX.** IX^e Congrès Ornithologique International, Rouen, 9 au 13 mai 1938. Compte rendu publié par Jean Delacour . . . Rouen. 543 pp. 1938.
- X.** Proceedings of the Xth International Ornithological Congress, Uppsala, June 1950. Edited by Sven Hörstadius. Almqvist & Wiksells, Uppsala. 662 pp. 1951.
- XI.** Acta XI Congressus Internationalis Ornithologici, Basel, 29. V.- 5. VI. 1954. Herausgegeben von Adolf Portmann und Ernst Sutter. Birkhäuser Verlag, Basel und Stuttgart. 680 pp. 1955.
- XII.** Proceedings of the XIIth International Ornithological Congress, Helsinki, 5. - 12. VI. 1958. Edited by G. Bergmann, K.O. Donner, L. v. Haartmann. Tilgmannin Kirjapaino, Helsinki. 2 vols. 820 pp. 1960.
- XIII.** Proceedings of the XIIIth International Ornithological Congress, Ithaca, 17-24 June 1962. Edited by Charles G. Sibley, Joseph J. Hickey and Margaret B. Hickey. Published by the American Ornithologists' Union. 2 vols. xvi + 1246 pp. 1963.
- XIV.** Proceedings of the XIVth International Ornithological Congress, Oxford, 24-30 July 1966. Edited by D.W. Snow. Blackwell Scientific Publications, Oxford and Edinburgh. xxiv + 405 pp. 1967.
- XV.** Proceedings of the XVth International Ornithological Congress, The Hague, 30 August - 5 September 1970. Edited by K.H. Voous. E.J. Brill, Leiden. viii + 745 pp. 1972.
- XVI.** Proceedings of the XVIth International Ornithological Congress, Canberra, 12-17 August 1974. Edited by H.J. Frith and J.H. Calaby, Australian Academy of Science, Canberra. xviii + 765 pp. 1976.
- XVII.** Acta XVII Congressus Internationalis Ornithologici, Berlin, 5-11. VI. 1978. Herausgegeben von Rolf Nöhring. Verlag der Deutschen Ornithologen-Gesellschaft, Berlin. Vol I, pp. 1-747; vol. II, pp. 756-1463. 1980.
- XVIII.** Acta XVIII Congressus Internationalis Ornithologici, Moscow, August 16-24, 1982. Edited by V.D. Ilyichev and V.M. Gavrilov. "Nauka", Moscow. Vol. I, pp. 1-576; vol. II, pp. 577-1335. 1985.
- XIX.** Acta XIX Congressus Internationalis Ornithologici, Ottawa, 22-29. VI. 1986. Edited by Henri Ouellet. Published for National Museum of Natural Sciences by University of Ottawa Press, Ottawa. Vol. I, pp. 1-1404; vol II, pp. 1405-2815. 1988.

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PROFESSOR HELMUT SICK 1910-1991**HONORARY VICE PRESIDENT
20TH INTERNATIONAL ORNITHOLOGICAL CONGRESS**

It was my pleasure and privilege to appoint my old friend, Helmut Sick, as one of the Honorary Vice-Presidents of the 20th International Ornithological Congress. On August 24, 1990, he wrote to tell me that he would be unable to participate in the Congress because he was seriously ill with malaria; he wrote: "You will be astonished - Malaria! I got my first malaria in 1941." He died on March 5, 1991.

Helmut Sick was born in Leipzig, Germany, in 1910 and studied science at German universities. He obtained the Ph.D. degree in ornithology in 1937 at the University of Berlin under the direction of Professor Erwin Stresemann. He then joined the staff of the Zoological Museum in Berlin and went to Brazil on an ornithological expedition just before the outbreak of World War II. He was not permitted to leave during the war and elected to remain in Brazil after the war. In 1946 he joined the Central Brazilian Foundation which was formed to explore the unknown interior of Central Brazil. Many of his publications on the birds of Brazil record results of this work over a period of seven years. He described his experiences in a popular book entitled "Tukani" (published in 1957 in German; 1959 in English) after his charming pet toucan. For the rest of his life he studied Brazilian birds and was a major influence in science and conservation in his adopted country. Helmut was the Brazilian delegate to the 11th IOC (1954) and was elected to the International Ornithological Committee at the 12th IOC in 1958 as the member from Brazil. I met him at the 1954 Congress in Basel, visited him in Rio de Janeiro in 1956, and we corresponded over the years. He was a productive and respected ornithologist, an accomplished artist, and a kind and valued friend.

Charles Sibley

CHARLES ALEXANDER FLEMING K.B.E., D.SC., F.R.S., F.R.S.N.Z. 1916 - 1987

Sir Charles Fleming was an eminent and valued member of the New Zealand Organising Committee for the Congress until his death in September 1987. The following tribute by Dr Peter C. Bull, Minutes Secretary to the Committee, is reproduced from the minutes of the 6th meeting of the Committee held in Wellington on 30 October 1987.

New Zealand lost one of its most distinguished scientists with the sudden death of Sir Charles Fleming at his home in Wellington on 11 September 1987 at the age of 71. Members of the New Zealand Organising Committee have particular reason to mourn his passing. Not only was he a personal friend of many of us, but he was also a highly respected and influential member of the Committee. As a distinguished scientist on the world scene, his presence and influence at the 19th International Ornithological Congress in Canada last year greatly helped New Zealand's successful bid to host the 20th Congress. Sir Charles was a former president of both the Royal Society of New Zealand and of the Ornithological Society (the two organisations sponsoring the 20th Congress) and his experience and sound judgement have been of great value to the Organising Committee. He will be sadly missed.

Sir Charles was born in Auckland and educated at Kings College and Auckland University where, after majoring in both geology and zoology, he gained his masterate with a thesis on prions (whalebirds). He joined the New Zealand Geological Survey in 1940 as an assistant geologist and remained in that organisation for the rest of his working life except for a period of war service as coastwatcher at the Auckland Islands. He returned to the Survey after the war and eventually became Chief Palaeontologist, a post that conveniently linked his geological and zoological interests. Declining further promotion, he concentrated his energies on research, the affairs of the Royal Society, and his varied cultural interests (music, art, languages and history).

His many outstanding research contributions in geology were matched by others in zoology - notably in ornithology, but also in biogeography, conservation, and the taxonomy and songs of cicadas. At the time of his death he had some 500 publications to his credit, including books, major research papers and numerous shorter articles. Apart from research, he took a very active part in the affairs of the Royal Society of New Zealand and was its president from 1962 to 1966. He also served a term (1968-69) as president of the Australian and New Zealand Association for the Advancement of Science.

The quality of his work earned him many honours, both at home and abroad. He was a Fellow of the Royal Society (one of very few New Zealanders to hold this distinction), a Foreign Member of the American Philosophical Society (the only New Zealand resident to be so honoured), a Corresponding Fellow of the American Ornithologists' Union, and a Fellow of the Royal Society of New Zealand. In 1977 he was made a Knight Commander of the Most Excellent Order of the British Empire (KBE) for services to science.

His ornithological contributions began with his classic study of the birds of the Chatham Islands (1939), closely followed by other major studies on the prions (1941)

and New Zealand flycatchers (1950). In studying the life history of the Silvereye (1943) he was one of the first New Zealanders to use coloured leg bands (home-made in those days) to identify individual birds in the field. Another pioneering effort, undertaken jointly with the late Dr K. Wodzicki, involved a census of the Gannet population of New Zealand (1952) by counting occupied nests shown on aerial photographs and checking the results by ground visits to some of the gannetries. This resulted in the first full census of any New Zealand seabird. Sir Charles had less opportunity for sustained ornithological research in later life, but he nevertheless kept up with current advances by extensive reading, and he watched and photographed birds whenever the opportunity offered. He enjoyed such activities immensely and his observations and experiences were often the subject of articles and lectures. Thus, in addition to his main ornithological papers, he has published several shorter ones plus many articles and short notes which together record a life-time's observations and thoughts on a wide range of ornithological topics. The Ornithological Society of New Zealand has particular reason to be grateful to Sir Charles. He was one of its founding fathers, a very active regional organiser in its early days, its president in 1948-49, and a faithful attender and contributor at meetings of the Wellington Branch over a period of some 40 years.

As a palaeontologist, Sir Charles was naturally interested in the geographical affinities of elements of the New Zealand fauna and flora, and in their appearance and disappearance throughout geological time, and he published extensively on these topics. He was particularly interested in the array of ancient forms (including several kinds of birds) preserved from extinction by New Zealand's long isolation, and he became very critical of the human mismanagement that had caused the recent extinction of some of these species and threatened the survival of others. Indeed, the proper conservation of New Zealand's native plants and animals, based on sound scientific principles, became a major concern for Sir Charles during the latter years of his life, and he fought long and hard to improve matters. Future generations will have much for which to thank him in this regard.

Those of us who were privileged to know Charles as a friend will remember him for his ready wit and agile mind, for his infectious enthusiasm in his appreciation and understanding of beautiful things both natural and man-made, and for his helpfulness and unobtrusive generosity. No less characteristic was his determination to use his intellectual abilities, possessions and reputation in the service of others, particularly in the promotion of good science and the conservation of natural resources for the physical and aesthetic enjoyment of future generations. The contributions of Sir Charles to the scientific and cultural life of New Zealand were indeed exceptional, but they were not his alone. Lady Fleming, a naturalist and historian in her own right, made these achievements possible through her dedication as Charles' adviser, secretary, field companion and competent manager of home and family. We extend our sympathy to Lady Fleming and her family, and also our grateful thanks for all she and Sir Charles have given us.

Peter Bull

XX CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

REPORT OF THE SECRETARY-GENERAL

The 20th International Ornithological Congress was held in Christchurch, New Zealand, over 2-9 December 1990. Following an Opening Ceremony and Civic Reception in the Christchurch Town Hall on the evening of 2 December, the major activities of the Congress took place on the campus of the University of Canterbury.

Patron

His Royal Highness, The Prince Philip, Duke of Edinburgh, agreed to be Patron of the 20th International Ornithological Congress. A message from Prince Philip to the Congress was read at the Opening Ceremony and is reproduced later in this volume.

Major sponsors

The two major sponsors of the Congress were the Ornithological Society of NZ (OSNZ) and the Royal Society of NZ.

History

As part of an international enquiry regarding possible venues for the 20th Congress, the President of the 19th Congress, the late Prof. Dr. Klaus Immelmann, wrote to New Zealand in September 1983. The present Secretary-General referred the matter to the Council of the OSNZ at its meeting in October 1983. In 1984 the Council established an investigative Congress Committee, comprising Ben D. Bell (convener), Brian D. Bell, Peter C. Bull and Sir Charles Fleming (adviser), to study the issue. In July 1985 the Congress Committee circulated a questionnaire to 85 NZ ornithologists seeking their views on a NZ Congress. Respondents strongly supported New Zealand placing an invitation for the 20th Congress in 1990, the favoured venue being Christchurch. In November 1985 the OSNZ Council authorised the committee to prepare a formal invitation to President Immelmann and the International Ornithological Committee (IOC). The OSNZ investigative committee was expanded to include B. Brown (ex officio President OSNZ), R.G. Powlesland, C.J.R. Robertson and H.A. Robertson. The NZ National Committee for the International Union of Biological Sciences (IUBS) and the Council of the Royal Society of NZ added their support for the invitation proposal. Both the Royal Society of NZ and the OSNZ agreed to act as major sponsors. A formal invitation prepared by the OSNZ Congress Committee was sent to President Immelmann and the Permanent Executive Committee in May 1986. A team of NZ ornithologists, together with their NZ agents, Conference Makers Limited of Auckland, attended the 19th Congress in Ottawa in June 1986 and New Zealand's invitation to host the 20th Congress in 1990 was approved by a large majority of members at the IOC meeting on 27 June 1986.

Local organisation

The NZ Organising Committee (NZOC) for the 20th Congress was formed in August 1986, drawing most of its membership from the OSNZ Congress Committee, which preceeded it. The NZOC handled planning of all aspects of the Congress within New Zealand. Eight members served on an Executive Committee which held regular meetings in Wellington. In 1987 the NZ Ornithological Congress Trust Board, comprising all eight members of the Executive, was formed as a charitable trust to handle financial and contractual aspects of Congress organisation. The NZOC held 13 meetings,

its Executive 65 meetings and the NZ Ornithological Congress Trust Board 6 meetings before the Congress. The NZOC delegated further organisational work to nine key subcommittees : Business Management, Christchurch Local Organising, Editorial, Excursions, Film Review, Grants Review, IOC–ICBP Liaison, Publications, and Publicity & Circulars.

Air New Zealand was appointed official carrier to the Congress. Conference Makers Limited of Auckland were appointed professional conference organisers and successfully handled a wide range of consultancy and organisational activities, including registrations, bookings, accommodation and tours.

“World of Birds” initiative

In late 1990 four major international events involving birds and natural history were coordinated in New Zealand under the theme “The World of Birds - a Southern Perspective”. These were the 20th International Ornithological Congress in Christchurch, the 20th World Conference of the International Council for Bird Preservation (ICBP) in Hamilton, the Pacific Festival of International Nature Films in Dunedin and the BirdPex '90 Stamp Exhibition in Christchurch. The coordinated registration, vehicle, tour and accommodation service, for all the conferences, was organised to provide a centralised service for all participants and encouraged participation in more than one event.

Membership

Members of the Congress comprised 1303 persons from 63 countries as follows:

Full members	877
Student members	131
Accompanying persons	135
Non-attending members	6
Staff volunteers	154

Opening and Closing Ceremonies of the Congress

The Opening Ceremony of the Congress took place in the Christchurch Town Hall on Sunday evening, 2 December. Following a traditional Maori challenge, members were welcomed by the Secretary-General who introduced the speakers of the opening addresses: Mr Tipene O'Regan, Chairman of the Ngai Tahu Trust Board; the President of the Ornithological Society of NZ, Brian D. Bell; the Mayor of Christchurch, Ms Vicki Buck; the President of the Royal Society of NZ, Professor John Dodd; the President of the 20th International Ornithological Congress, Professor Charles G. Sibley; the NZ Minister of Conservation, the Hon. Denis Marshall MP, who also delivered the message from the Congress Patron, H.R.H. The Prince Philip; and Sir Edmund Hillary, who formally opened the Congress.

A Reception and Dinner hosted by the Mayor and City of Christchurch, was held in the Christchurch Town Hall after the Opening Ceremony. Over 1000 members and guests attended, which helped to establish a friendly and cordial atmosphere for the rest of the Congress week.

The Closing Ceremony was held in the display pavilion at the University of Canterbury on Saturday, 8 December, after the last oral presentation. The President, Professor Charles Sibley, announced Vienna, Austria, as the venue for the 21st International Ornithological Congress in 1994, with Christopher M. Perrins (United Kingdom)

as President. Professor Sibley also announced the names of new officers of the 21st Congress and the names of 65 ornithologists, from 35 countries, elected to the International Ornithological Committee. The Secretary-General paid a tribute to the late Sir Charles Fleming (New Zealand) in recognition of his service to ornithology and the NZ Organising Committee. The President and Secretary-General expressed their warmest thanks to all those who had contributed much to make the Congress such a memorable and successful event. The 20th International Ornithological Congress was then formally closed by the President.

Exhibits

A special exhibit on New Zealand birds was provided at the Congress venue by the Canterbury Museum, allowing visiting ornithologists to examine a range of skins of New Zealand birds. Commercial and institutional exhibits were sited in the Pavilion near the poster paper exhibits. As part of the "World of Birds" initiative the Christchurch Philatelic Society held an international stamp exhibition (BirdPex '90) in the Student Union building at Canterbury University during the Congress. Further details of exhibits are given in the Supplement (Programme and Abstracts).

Receptions and Conversazioni

Oxford University Press, in conjunction with the Royal Australasian Ornithologists Union (RAOU), held a reception to launch *"The Handbook of Australian, New Zealand and Antarctic Birds"* on Wednesday evening. The Secretary-General introduced the Minister of Conservation, the Hon. Denis Marshall MP, who launched the first two volumes of this major new work on the avifauna of the region. Other receptions included those hosted by the President and Mrs Sibley at the Chateau Blanc (Wednesday); by the RAOU to invest Brian D. Bell (NZ) as a Fellow of the RAOU (Friday); by the NZ Organising Committee for members of the PEC and assisted delegates (Friday). Conversazioni held during the Congress were for the Frank Chapman Memorial Fund (Tuesday) and the British Ornithologists Union (Wednesday).

Local Activities

Early-morning and day excursions were well attended during the Congress. On Thursday, 6 December, a Field Day and High Country Fair was held at the Mount Hutt Station Resort, near Methven. Most members went on bird excursions before arriving at Mount Hutt later in the day. The Methven Lions Club and residents of the Mount Hutt district delighted members with displays and the informal entertainment of a high-country fair. The day ended with a relaxing social and barbecue featuring some of the best of NZ country fare and country-style dancing. The final local activity of the Congress, the closing banquet, was held on Saturday evening, 8 December, and was attended by over 700 members and guests.

Pre- and Post-Congress Tours

Under the "World of Birds - a Southern Perspective" theme an integrated programme of pre-Congress and post-Congress group tours was offered to Congress members in and around New Zealand. Fifteen main tour routes were used to give members a chance to view a wide range of New Zealand birds, habitats and landscapes. These included visits to major national reserves, such as Little Barrier, Stephens and Codfish Islands. As alternatives to conducted group tours, self-drive tours, using cars or motor camper vans, were offered.

A major event was to have been a subantarctic island cruise on board the brand new M.V. Frontier Spirit from 9-22 December 1990. Unfortunately, due to damage sustained by the ship in a cyclone in Fiji during November, the Frontier Spirit cruise was cancelled. Fortunately passage on an alternative subantarctic cruise with the M.V. World Discoverer was arranged by 77 Frontier Spirit passengers.

Scientific Programme

The President hosted a meeting of members of the international Scientific Programme Committee (SPC) at Tiburon, Marin County, California, in November 1987. All members of the SPC were able to attend the meeting, chaired by Dr Peter Berthold (Germany). The SPC reviewed over 300 proposals for symposia and other presentations, then allocated the programme of plenary speakers, symposia topics and conveners. In consultation with Dr Berthold, review and allocation of contributed papers (oral and poster), round table discussions and special interest groups was carried out in New Zealand at a meeting of local SPC members convened by Dr Murray Williams (Vice-Chairman).

The resulting scientific programme of the 20th International Ornithological Congress followed the broad format of its predecessors. Six major ornithological themes were adopted for the plenary and symposia sessions: Systematics, Evolution and Ornithogeography; General Biology; Behaviour; Ecology; Physiology; and Applied Ornithology.

The scientific programme included over 800 contributions including 7 plenary papers; 240 papers in the 48 symposia; 276 oral contributed papers; 233 contributed poster papers; 31 round-table discussions; and 10 special interest groups. Further details are given in the Supplement (Programme and Abstracts).

Film Programme

A programme of recent ornithological and natural history films was screened through the Congress week in the Ngaio Marsh Theatre at the University of Canterbury. Under the "World of Birds - a Southern Perspective" theme, Congress organisers and Television New Zealand (TVNZ) cooperated in the selection of film material. A total of 39 films for the Congress programme was selected from bird films submitted to TVNZ for the Pacific Festival of International Nature Films in Dunedin. Further details are given in the Supplement (Programme and Abstracts).

Report of the Permanent Executive Committee

The Permanent Executive Committee held five meetings in Christchurch on 2, 3, 4, 5 and 7 December. All members, with the exception of B.K. Follett (UK), S. Haftorn (Norway) and C. Érard (France), were able to attend. The topics discussed were reported on at the meetings of the International Ornithological Committee on 4 and 7 December. On 8 December an informal meeting of the old (1986-1990) and new (1990-1994) Executive Committees was held.

Report of the International Ornithological Committee

The International Ornithological Committee (IOC) met on 4 and 7 December. Both meetings were chaired by the President, Professor Charles Sibley. Fifty members were present on 4 December and 49 members on 7 December.

At the first meeting reports were received from the President, Secretary-General, Chairman of the Scientific Programme Committee and Permanent Secretary of the IOC. The President outlined issues discussed by the Executive Committee at its three meetings over 2-4 December.

Dr John Dittami and Dr Hans Winkler gave a slide presentation on the proposed venue and facilities that Austria was offering for the 21st Congress in August 1994. On the recommendation of the Executive, the IOC voted to accept Vienna as the venue for the 21st Congress (no other formal invitations having been received).

The Permanent Secretary introduced proposed amendments to the Statutes & By-Laws for consideration at the second IOC meeting. The Secretary-General tabled reports from the three IOC Standing Committees: Ornithological Nomenclature (Professor W.J. Bock); Coordination of Seabird Research (Dr David Nettleship); Applied Ornithology (Professor Dr V.D. Ilychiev and Dr R.W. Peterson). Dr Nettleship and Professor Bock addressed their Standing Committee reports. All three reports appear later in this volume.

Professor Burt L. Monroe Jr. tabled a report from P. William Smith, Convener of Round Table Discussion No. 1 - Standardisation of English Bird Names. That discussion on 3 December had up to 60 participants and had voted to recommend to the IOC that it appoint Professor Monroe as convener of a working group on Standardisation of English Bird Names, with power to co-opt members to represent the broadest possible range of opinion and geography. The IOC voted to approve the establishment of such a working group which should report through the Permanent Secretary to the 21st Congress in 1994. It was felt such a group should not be limited to only a few people but should be widely representative. The IOC also voted to establish an international group to standardise French bird names under the Chair of Dr Henri Ouellet. Dr Ouellet outlined progress of the working group to date.

A Resolutions Committee was appointed to consider resolutions presented at the second IOC meeting. Committee members were W.J. Bock (USA), E. Bucher (Argentina) and J. King (USA). A Nominations Committee established by the Executive to receive nominations for members of the IOC was endorsed. The members were P. Berthold (Germany), H. Ouellet (Canada), C.M. Perrins (UK), L. Short (USA) and L. Tomialojc (Poland).

At the second meeting Dr Hans Blokpoel, at the invitation of the President, reported on the first term of the Standing Committee on Applied Ornithology. The officers, Executive Committee and new members of the IOC were then elected.

IOC approved the following executive positions for the next Congress: Karel H. Voous (Netherlands) as Honorary President, Christopher M. Perrins (UK) as President, Svein Haftorn (Norway) as Vice-President, and Walter J. Bock as Secretary of IOC.

The elected membership of the Executive Committee was raised from eight to ten. Accordingly, three members were re-elected to the Executive Committee (EC): Peter Berthold (Germany), Enrique H. Bucher (Argentina) and E.N. Kurochkin (USSR); and seven new members were elected: Asha Chandola-Saklani (India), Hiroyuki Morioka (Japan), Cynthia Carey (USA), Henri Ouellet (Canada), Richard Liversidge (South

Africa), Jacques Blondel (France) and Murray J. Williams (New Zealand). Other members of the EC ex officio are the President (Chairman), Vice-President, Secretary-General, Secretary, immediate Past President and immediate Past Secretary-General. Sixty two new members of the International Ornithological Committee were elected and three were re-elected:

Argentina	Manuel Nores
Australia	Jiro Kikkawa, Phillip Moors, Pat Rich
Austria	John Dittami, Ellen Thaler, Hans Winkler
Belgium	Andre Dhondt, Michel Louette
Brazil	Paulo Antas
Canada	Jon C. Barlow, Fred Cooke, Raymond McNeil, David N. Nettleship
Chile	Fabian Jaksic
Colombia	F. Gary Stiles
Cuba	Orlando H. Garrido-Calleja
Czechoslovakia	Karel Hudec (re-elected), Aladar Randiik, Andrev Stollman
Eire	Oscar Merne
Finland	Olavi Hilden
Germany	Roland Prinzinger, Klaus Schmidt-Koenig, Rosi Wiltschko
Hungary	Lajos Sasvári
Iceland	Arnthor Gardarsson (re-elected)
India	Manjit S. Dhindsa, Zafar Futehally, S.Ali Hussain
Israel	Yoram Yom-Tov
Italy	Fernando Spina, Carlo Violani
Japan	Juzo Fujimaki, Hiroyoshi Higuchi
Kenya	Nathan Gichuki
Netherlands	Arie L. Spaans, Gert Zweers
New Zealand	John L. Craig, Murray J. Williams
Norway	Tore Slagsvold
P. Republic of China	Zheng-jie Zhao, Guang-mei Zheng
Poland	Tomasz Wesolowski
Republic of China	Lucia Liu Severinghaus
Rumania	Laszlo Kalaber
South Africa	Timothy M. Crowe, Alan Kemp, W. Roy Siegfried (re-elected)
Sweden	Staffan Ulfstrand
Switzerland	Lucas Jenni
Uganda	Derek Pomeroy
USSR	Alexander V. Andreev, R. L. Potapov, Yuri V. Shibaev
United Kingdom	John P. Croxall, George M. Dunnet, Peter R. Evans
USA	John W. Fitzpatrick, Richard T. Holmes, Dominique G. Homberger, Ellen D. Ketterson, Burt L. Monroe Jr., John C. Wingfield
Zimbabwe	Peter J. Mundy

Changes to the Statutes and By-Laws (recommended by the Executive) were adopted by a vote of IOC. General changes included dropping the term "Permanent" from

“Permanent Executive Committee” and “Permanent Secretary” and the removal of sexist language. Most changes were to better accommodate the new position of Secretary of the IOC, with formal division of the duties and responsibilities of the Secretary-General and the Secretary, (as detailed under the “Statutes and By-Laws” section of this volume). A further change in the By-Laws is the new requirement for advance notice to be given by nations intending to offer invitations to host a future Congress.

The Secretary-General informed the IOC of his recent discussions with the Director of the International Council for Bird Preservation (ICBP). The relationships between the IOC and ICBP were discussed, particularly in relation to the IOC Committee on Applied Ornithology and the scientific programmes of future Congresses.

Resolutions

The following Resolutions were adopted by the IOC at its second meeting on 7 December after review by the Resolutions Committee and the Executive:

Resolution 1. Submitted by the Standing Committee on Ornithological Nomenclature:

The International Ornithological Committee at its meetings during the XXth International Ornithological Congress, Christchurch, New Zealand, 2-9 December 1990 congratulates and supports the International Commission on Zoological Nomenclature in its efforts to increase continuity of zoological nomenclature by the conservation and stabilisation of established names, and directs its Standing Committee on Ornithological Nomenclature to assist the International Commission on Zoological Nomenclature in these efforts. The International Ornithological Committee recognises the pioneering actions of the Standing Committee on Ornithological Nomenclature in developing a list of available family-group names of birds and urges this committee to undertake similar projects on genus-group and species-group names of birds.

Resolution 2. Submitted by T. Crowe:

The members of the International Ornithological Congress protest in the strongest possible terms the decision by the executive of the British Museum (Natural History) [BM(NH)] to abolish the research-oriented posts in the museum's Sub-department of Ornithology. The bird collection at the BM(NH) is one of the most comprehensive resources of its kind internationally, and the BM(NH) scientists utilising this resource have, in the past, made major contributions to the areas of systematic biology and biogeography. A scientifically revitalised Sub-department of Ornithology could do the same in the future. It is unrealistic to expect that scientists visiting from other institutions can fill the gap created by the abolition of these research posts, especially if they are required to pay “bench fees” to use the collection. Therefore, we request that the BM(NH) executive and Board of Trustees consider reinstating research posts and rescinding the implementation of bench fees (at least for bona fide scientists) in its Sub-department of Ornithology.

Resolution 3. Submitted by the Israeli ornithologists:

We, the amateur and professional ornithologists participating at the 1990 XXth International Ornithological Congress, are deeply concerned about the possible im-

pact on millions of migrating birds by the immense Voice of America relay station projected for construction in the Aravah Valley. We fear the following effects of this station on birds:

1. Collision with the huge 140-200 meter high towers, meteorological antennas and mazes of cables.
2. Overheating of approaching and roosting birds by high-intensity short wave radiation emitted by 16 500kw transmitters.
3. The as yet unknown effects of electromagnetic radiation on orientation, navigation and behaviour of migrating birds.

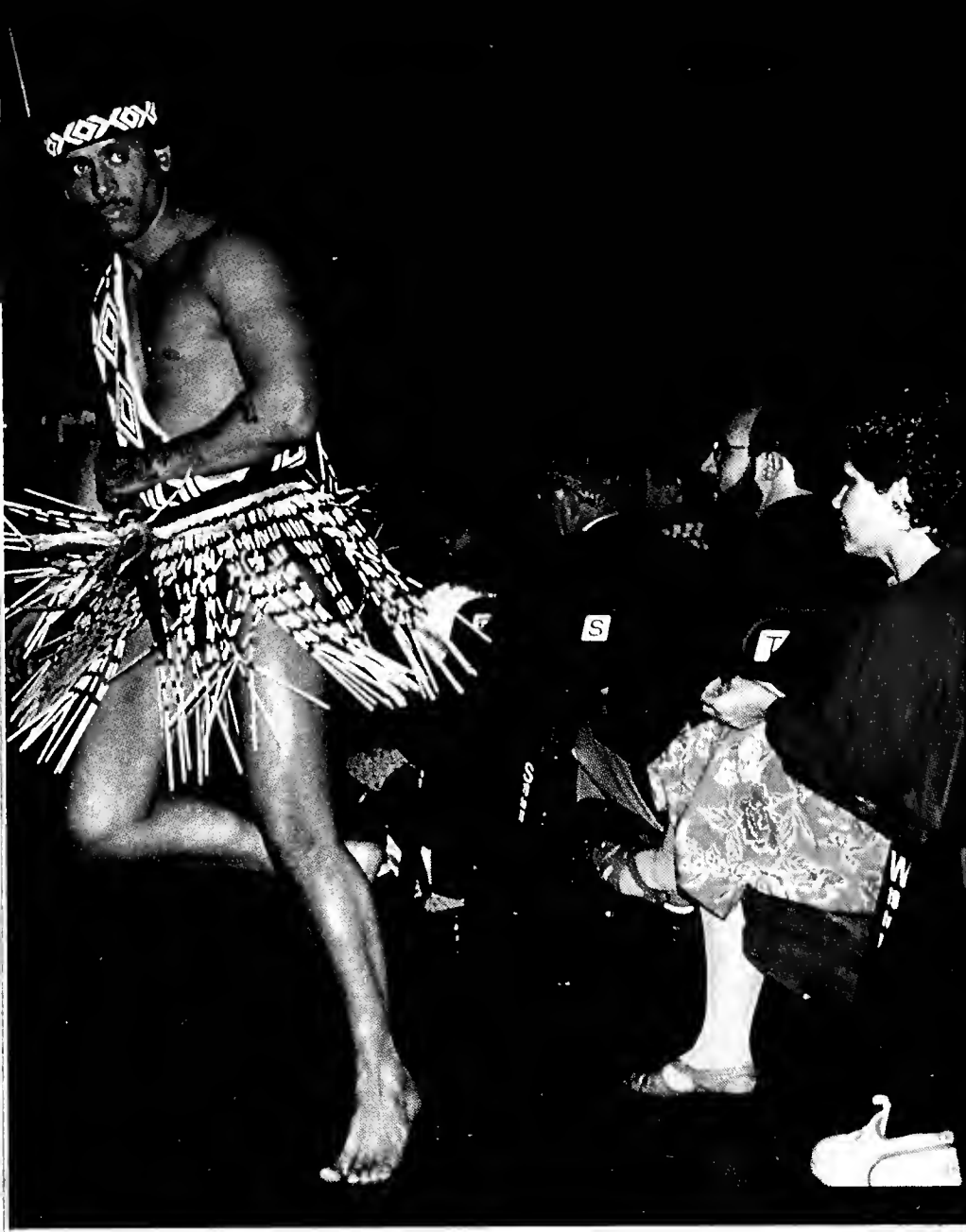
We strongly urge the governments of Israel and the United States of America to stop all activities connected with the implementation of this project until thorough, independent environmental impact assessments are studied and completed, and the relevant recommendations are adopted.

Resolution 4. Submitted by the Resolutions Committee:

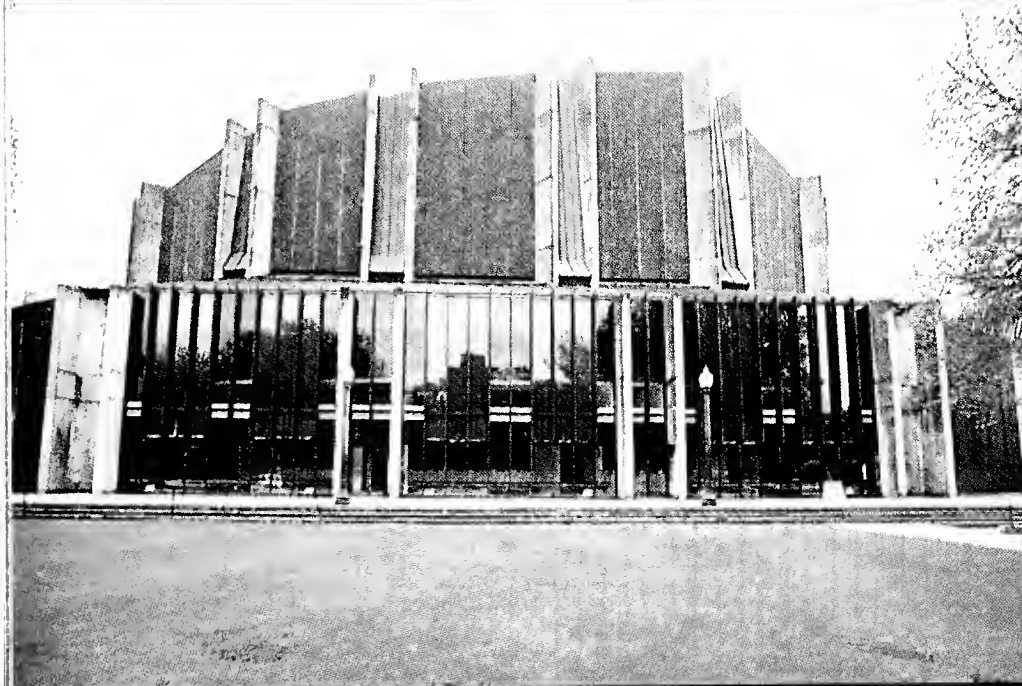
- A. WHEREAS the participants of the XXth International Ornithological Congress have enjoyed a stimulating programme, rich in professional and social variety, in a comfortable and congenial setting, AND WHEREAS the efficient and hospitable arrangements and their execution bespeak thorough, thoughtful, and wise planning, THEREFORE BE IT RESOLVED that the International Ornithological Committee, on behalf of the participants of the XXth International Ornithological Congress, convened in Christchurch, New Zealand, extends its deepest thanks to the New Zealand Organising Committee, and their associates and sponsors, for their part in making the XXth International Ornithological Congress a rich and memorable experience.
- B. WHEREAS the participants of the XXth International Ornithological Congress have experienced a rewarding scientific programme of exceptional variety, depth and quality, AND WHEREAS the development and management of such an excellent programme, including the timely publication of its Proceedings can result only from experienced insights, skillful negotiations, and long effort, THEREFORE BE IT RESOLVED that the International Ornithological Committee, on behalf of the participants of the XXth International Ornithological Congress, extends its special thanks to the Scientific Programme Committee and its advisors for their role in ensuring the scientific success of the XXth International Ornithological Congress.
- C. WHEREAS the contributions made by all those who took part in the development and management of the XXth International Ornithological Congress were indispensable, but WHEREAS the guidance and coordination of their efforts required the skills and labour of special leaders, THEREFORE BE IT RESOLVED that the International Ornithological Committee, on behalf of the participants of the XXth International Ornithological Congress, extends its heartfelt thanks to Ben D. Bell, Murray Williams, Chris Robertson and Peter Berthold for fulfilling so well their special roles in making the XXth International Ornithological Congress a first class, world-class event.

Funding of the Congress

Unlike its immediate predecessors, the NZ organising committee was not supported by a major government grant to fund necessary Congress planning and organisation. However, various government organisations provided important services and assistance, most notably the Department of Conservation's Science and Research Division



OPENING CEREMONY - 1. Maori challenge. 2. Official party arrives. 3. Vicki Buck (Mayor, Christchurch) & President. 4. Prof. Charles Sibley (President). 5. Tipene O'Regan (Chair. Ngai Tahu Trust Board). 6. L to R. Sir Edmund & Lady Hillary; Hon. D. Marshall; Prof. J. Dodd (Pres. Royal Soc. of NZ); Brian Bell (Pres. Ornithological Soc. of NZ). 7. Hon. Denis Marshall (Minister of Conservation). 8. Christchurch Town Hall.





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SCIENTIFIC PROGRAMME

1. Lecture audience. 2. Cynthia Carey (Plenary). 3. Ian Atkinson (Plenary). 4. Enrique Bucher (L) and staff preparing for Plenary. 5. Murray Williams (Vice-Chair, Scientific Programme Committee). 6. Poster Paper Pavilion.



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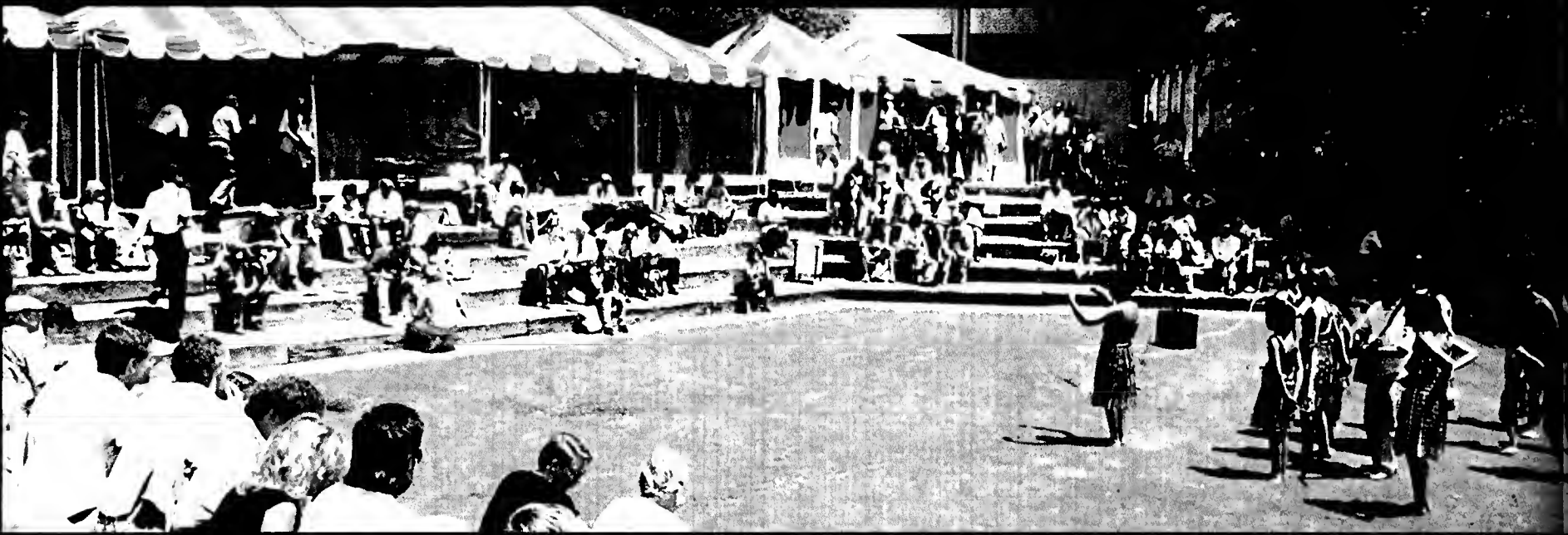


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1. Part of Exhibitions. 2. Poster paper evening session. 3. Commercial Exhibits. 4. Peter Berthold (Chair, Scientific Programme Committee). 5. John Dittami (L) (as actor) during Plenary of John Craig (R).





IN
BETWEEN
THE
LECTURES





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EXCURSIONS

1. Lake Ellesmere. 2. Heathcote-Avon estuary;
3. Field excursion group. 4. High Country Cook
Out. 5 & 6. Mount Hutt High Country Fair.
7. Whitewash Head excursion. 8. Wind storm on
the Upper Rakaia River.



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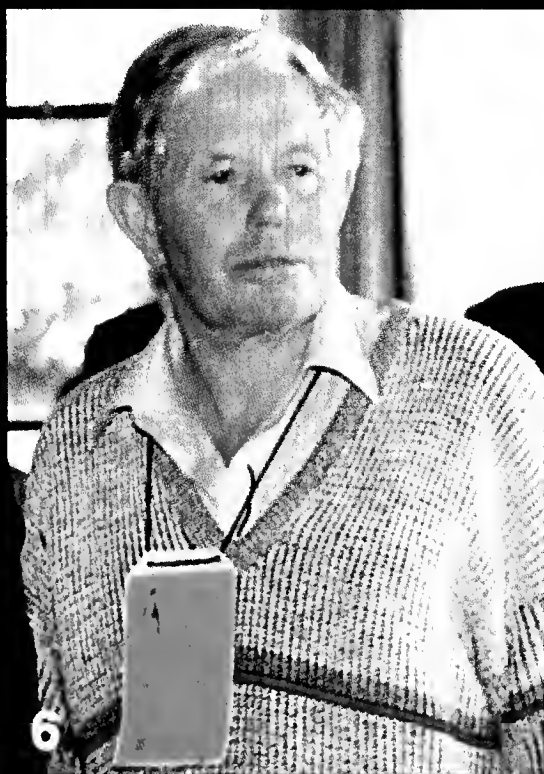
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STAFF - 1. Conference Management & Registration. **2.** Roderick Cossee, Sue Keall, Paul Westerbeke of 'Communications Centre'. **3.** Airlines, Cruise & Tours Desk. **4.** Congress Shop in the Pavilion. **5.** Two of the 148 Volunteer Staff. **6.** Brian Bell (Chairman, Tours Organising Committee). **7.** The Accommodation Desk.



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CLOSING CEREMONY - 1. President & Lesley Fairbairn (Conference Makers Limited). 2 & 3. Members of NZ and Local Organising Committees. 4 & 6. Congress members & Volunteer staff. 5. Bob Thomson (Chair. Local Organising Committee). 7. President & Christopher Robertson (Congress Business Manager). 8. L to R. N Kuroda (Hon. President); C Sibley (President); J Pinowski (Vice-Pres.); Ben Bell (Secretary-General); W Bock (Permanent Secretary IOC). Inset. L to R. Gillian Bell, Gillian Robertson, Frances Sibley, Christopher Perrins, Peter Berthold.



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THE BANQUET

in Wellington and the Ecology Division of the Department of Scientific and Industrial Research (now DSIR Land Resources). The Congress was an official project of the NZ 1990 Commission who gave generous financial support. The Science and Research Distribution Committee of the NZ Lottery Board provided a major grant towards the publication of the Proceedings. Support for the Secretary-General and for editing the Acta was provided by Victoria University of Wellington. Other sources of revenue included proceeds from membership fees, rental of display spaces during the Congress, commissions from tours, sales and accommodation, grants or loans from the OSNZ, Royal Society of NZ, Air New Zealand and the Todd Foundation. A full list of sponsors is given in the Supplement p. 28.

Acknowledgements

The organisation of such a large Congress has been a major team effort and many persons, both overseas and within New Zealand, have contributed in numerous ways to its success.

The New Zealand Organising Committee expresses its thanks to His Royal Highness, The Prince Philip, Duke of Edinburgh, for agreeing to act as the Patron of the Congress.

I have had a close and constructive working relationship with the President throughout the planning of this Congress. I thank Professor Sibley for his constant support and wise counsel. I am also appreciative of the work carried out by other overseas colleagues on behalf of the Congress, particularly by Peter Berthold (Germany) and members of the Scientific Programme Committee; and by Walter Bock (USA), Permanent Secretary of the IOC. I am indebted to former President, the late Klaus Immelmann (Germany) and former Secretary-General, Henri Ouellet (Canada), for assistance during the early days of Congress bidding and organisation.

To a substantial degree, the Congress owes its success to the unstinting support of numerous people in New Zealand, most of whom worked in a voluntary capacity and well beyond the call of duty. In particular, I thank our army of staff and volunteers - including members of the Ornithological Society of NZ, students and tour guides - who worked in many parts of the country on our behalf. The particular responsibility of successfully planning and organising the Congress rested on the shoulders of the various organising committees in New Zealand and I thank all of them for their hard work.

The eight member Executive Committee in Wellington were the core management team for the Congress and I wish to record my thanks to them for their considerable individual and collective efforts. Brian Bell, convener of the Excursions Subcommittee, organised an excellent tours programme using his wide knowledge of New Zealand and its birds; Peter Bull, Minutes Secretary, skillfully and meticulously recorded the minutes of our many meetings, providing the Congress archives with an exemplary record; Ralph Powlesland, convener of the Publications Subcommittee, developed and maintained our international mailing database, and played a key role in the production of the two circulars and Programme and Abstracts volume; Chris Robertson, convener of the Business Management Subcommittee, took on an enormous area of responsibility, handling a wide range of business activities, including financial management, liaison with Conference Makers Limited, and the complex negotiations

regarding the Southern Ocean Cruise; Hugh Robertson, convener of the Circulars and Publicity Subcommittee, was responsible for Congress circulars and publicity, promoting the Congress in New Zealand and overseas; Murray Williams, Vice-Chairman of the Scientific Programme Committee, competently and amicably handled scientific programme matters, including liaison with SPC Chairman, Peter Berthold, with symposia conveners, and other contributors; and Sue Usher, Royal Society of NZ representative, offered wise counsel on a wide range of business and planning issues, and represented at executive level our senior sponsor, the Royal Society of NZ.

I also extend my thanks to other members of the NZ Organising Committee: the late Sir Charles Fleming, for support and advice; Beth Brown, representing the OSNZ; Mick Clout, representing the 20th ICBP World Conference organising committee; Leslie Fairbairn, representing Conference Makers Limited; Audrey Hudson, our accounting advisor; Paul Sagar and Bob Thomson, successive conveners of the Christchurch Local Organising Subcommittee; and Brian Wybourne, representing the Council of the Royal Society of NZ and the academic community in Christchurch.

Central planning by the Wellington Executive was complemented by much work in Auckland by our professional consultants, Conference Makers Limited, and in Christchurch by the Local Organising Subcommittee. The experience, sound advice and professionalism provided by Leslie Fairbairn and her colleagues at Conference Makers Limited was an essential ingredient in the smooth running and success of the Congress, and I warmly thank them for carrying out their role as professional conference organisers so well. The organisational demands of such a large Congress were immense and theirs was a job well done. Another substantial organisational burden fell on the Christchurch Local Organising Subcommittee, particularly in the latter part of 1990. I thank all members of that committee for their hard and often demanding work. Theirs was a critical role and I express thanks to Patricia Bell, Chris Challies, Ian McLean, Colin O'Donnell, Paul Sagar, Eric Spurr, Jill West, Kerry-Jane Wilson for their contributions. I especially thank their convener - Bob Thomson - for his excellent leadership and support.

I thank Ian Atkinson, Bill Lock, Ralph and Mary Powlesland for assisting the Editorial Subcommittee in the large proof-reading exercise necessary for the preparation of these Proceedings; and Sue Keall for taking on the task of Minutes Secretary to the NZ Executive Committee during 1991.

My thanks also go to many others who assisted in Congress organisation in a variety of ways. These include: Dr Richard Sadleir, Director of Science and Research, Department of Conservation; Professor John Wells, School of Biological Sciences, Victoria University of Wellington; Dr Malcolm Crawley, Director of the former Ecology Division, Department of Scientific and Industrial Research; the invited speakers at the Opening Ceremony - Mr Tipene O'Regan, Ms Vicki Buck, Professor John Dodd, the Hon. Denis Marshall and Sir Edmund Hillary. Finally, I thank our many sponsors for their support and confidence in our organisational and planning endeavours.

Ben D. Bell
Secretary-General

REPORTS OF THE STANDING COMMITTEES OF THE INTERNATIONAL ORNITHOLOGICAL COMMITTEE

The reports of the three Standing Committees were submitted to the Secretary-General in 1990 prior to the 20th International Ornithological Congress.

REPORT OF THE STANDING COMMITTEE ON ORNITHOLOGICAL NOMENCLATURE

At the 18th International Ornithological Congress (Moscow, 1982), the Standing Committee on Ornithological Nomenclature (SCON) passed a resolution to begin work on a historical analysis of avian family-group names. This project was essential because of the changes in the rules of zoological nomenclature in the 1961 Code of Zoological Nomenclature which threatened continuity of several well-established avian family-group names. This project was well under way by the 19th Congress (Ottawa, 1986) at which time the SCON passed several resolutions which were presented to the International Ornithological Committee (IOC) and were passed at the first meeting of that body (the latter action was not mentioned in the report of the IOC in the Proceedings of the 19th Congress). This project on the history and status of avian family-group names is basically completed and will be submitted for publication as soon as corrections and suggestions are received from members of the SCON and other interested ornithologists and the final proof reading is completed. Copies of the penultimate draft of this monograph will be available to interested ornithologists at the 20th Congress at the display of materials on zoological nomenclature.

It is hoped that the "History and Nomenclature of Avian Family-Group Names" will be in press during 1991. After it is published an application will be submitted to the ICZN proposing that this publication be accepted as the base line for avian family-group names. Only the names included in this list with the authors and dates of publication as given will be available for zoological nomenclature. Names published prior to its publication but overlooked will be treated as unavailable for zoological nomenclature.

An information table on zoological nomenclature with materials provided by the Secretariat of the International Commission on Zoological Nomenclature will be set up at the Congress. With the support of a number of ornithologists, Walter Bock was elected as a Commissioner of the International Commission on Zoological Nomenclature in 1988. This provides an important direct link between the Standing Committee on Ornithological Nomenclature and the International Commission on Zoological Nomenclature (ICZN). The SCON functions as a specialist committee on avian nomenclature for the ICZN.

The ICZN met during the ICSEB, Maryland, July 1990; Walter Bock, as a Commissioner, took part in this meeting and reported on some of the more significant decisions. Perhaps the most important result of this meeting was the decision by the ICZN to develop several methods to insure continuity of nomenclature. These methods will include the reintroduction of a stronger and automatic regulation to conserve established names versus forgotten senior synonyms (a return to a form of the 50 year rule), and the development of lists of known available names with dates of precedence, etc. The list of avian family-group names will be among the first, if not the first, of these lists for zoological names. Once such a list is established and approved by the ICZN, names on the list and those published in the future will be the only ones available for that group of animals. Any names not on the list cannot be used without application to and approval by the ICZN. These actions by the ICZN and the proposed amendments to the Code are most positive steps by the ICZN toward continuity of nomenclature. The system of using endings "i/ii" for male personal names will be rationalised. Gender agreement of generic and specific names will be simplified. The

stem for family group names formed from Greek words ending in "is" or "es" will be simplified; the proposed rule will be that such names would be treated simply for any family-group name in which the grammatically correct form is not in common usage, e.g., Drepanididae, type genus *Drepanis*.

The ICNZ also considered briefly the question of extending the Code to names above the family-group, and still expressed the strong opinion that these names should be excluded from the Code. Problems still exist for many names in cladistic classifications in which the authors are unclear as to whether the groups belong to the family-level or to the order-level.

A new project was proposed for the SCON to begin work on a list of available generic-group names for birds. Such a list has been started by Murrey Bruce. Walter Bock will discuss with M. Bruce, methods for continuing this list under the auspices of the SCON. A report will be presented at the 1994 meeting of the committee.

Burt Monroe moved and David Holyoak seconded a motion that the IOC adopt a resolution supporting the ICZN in its actions to insure the stability and continuity of zoological nomenclature and to direct the SCON to assist the ICZN in these efforts.

RESOLUTION: "The International Ornithological Committee at its meetings during the XXth International Ornithological Congress, Christchurch, New Zealand, 2-9 December 1990 congratulates and supports the International Commission on Zoological Nomenclature in its efforts to increase continuity of zoological nomenclature by the conservation and stabilization of established names, and directs its Standing Committee on Ornithological Nomenclature to assist the International Commission on Zoological Nomenclature in these efforts. The International Ornithological Committee recognizes the pioneering actions of the Standing Committee on Ornithological Nomenclature in developing a list of available family-group names of birds and urges this committee to undertake similar projects on genus-group and species-group names of birds".

Burt Monroe moved and Richard Schodde seconded a motion giving a vote of thanks for the outstanding efforts of Walter Bock in compiling the list of avian family-group names and writing a history of these names and of zoological nomenclature during the period in which the new regulations covering family-group names were developed.

At its meetings during the 20th International Ornithological Congress, the SCON considered a number of existing and pending applications on avian names before the ICZN and discussed several new cases.

- a) A major application is one to be prepared by Walter Bock on avian family-group names based on the analysis of these names as mentioned above. Basically this application will request that the ICZN accept the list of the valid names and their synonyms for the currently recognized family-level taxa of Recent (non-fossil) birds and the decisions contained within it, including the date of publication and author of the valid names and their synonyms, names to be conditionally conserved and suppressed, and names which are not available for purposes of zoological nomenclature or which are objectively invalid. This list will serve as the base for all future nomenclatural actions on avian family-group names for living birds. The date of this base line will be 1 January 1991.

- b) Other applications cover nomenclatural problems in the family-group names Phororhacidae and *Phororhacos*, Hydrobatidae and Threskiornithidae, and in the genera *Macronectes*, *Catharacta*, *Carpophaga* and *Serresius*, *Rallus*, *Cacatua*, *Geospiza*, *Creadion*, *Calyptorhynchus*, *Dendrocygna*, *Eurystomus*, *Calidres*, and *Corvus*.
- c) The SCON urges the ICZN and its Secretariat to speed the process by which applications are processed and published, and final action is taken by the ICZN. Further the SCON urges the ICZN and its Secretariat to increase its use of the SCON as a specialist advisory committee and to submit all applications dealing with birds to the SCON for its consideration. Further ornithologists are strongly urged to interact with the SCON to discuss possible nomenclatural matters and in the development of applications to submit to the ICZN. W. Bock was asked to raise these concerns at the meeting of the ICZN in September 1991.

Members of the SCON appointed by the President Charles G. Sibley for the period 1986-1990 were: Walter J. Bock (Chairman), Pierre J. Devillers, Christian Énard, David Holyoak, Ernst Mayr, Gerlof F. Mees, Burt Monroe, Hiroyuki Morioka, Henri Ouellet, Richard Schodde, L.S. Stepanyan, Karel H. Voous, George Watson, David Wells and Hans Wolters.

Respectfully submitted for the Standing Committee on Ornithological Nomenclature of the International Ornithological Committee.

Walter J. Bock
Chairman, SCON

Members of the Committee on Ornithological Nomenclature for 1990-94 are:

Walter J. Bock (USA), Chairman*
Murray D. Bruce (Australia)*
David Holyoak (United Kingdom)*
Ernst Mayr (USA)
Gerlof F. Mees (Netherlands)*
Burt L. Monroe Jr (USA)*
Hiroyuki Morioka (Japan)*

Henri Ouellet (Canada)*
D. Stefan Peters (Germany)*
Richard Schodde (Australia)*
L. S. Stepanyan (USSR)
Karel H. Voous (Netherlands)
David Wells (Malaysia)
Hans E. Wolters (Germany)

* Members attending the meetings of the SCON at the XX International Ornithological Congress.

REPORT OF THE STANDING COMMITTEE FOR THE COORDINATION OF SEABIRD RESEARCH

The Standing Committee for the Coordination of Seabird Research (SCCSR) of the International Ornithological Committee (IOC) is an international group of marine bird biologists appointed by the President of the IOC. The SCCSR was established in 1966 with the principal aim of providing a mechanism for enhanced information exchange and integration of research on seabirds worldwide. That liaison function has traditionally been achieved through organised discussions and presentations at each congress, culminating with the presentation of a special interest symposium as part of the formal IOC Scientific Programme.

One major outcome of the open meeting at the 19th Congress in Ottawa in June 1986 and discussions that followed, was the clear desire by all participants (committee members and others) to see more emphasis placed on action-orientated activities to be pursued *between* congresses. With that as a goal, the development of working groups was initiated to undertake specific review exercises (based on consensus of research needs) including the formulation of special symposia and workshops. Final decisions resulted in the establishment of four working groups - "Seabirds-at-sea", "Bibliographies", "Nomenclature", and "Technological innovations" - and a task force to solicit recommendations on possible symposia titles for the SCCSR's official contribution to the 20th Congress. The following is a brief summary of major activities of the working groups and task force, and the overall accomplishments of the standing committee during the review period, 1986-1990.

IOC-SCCSR Special Symposium

After considerable input and discussions by committee members and non-members between 1986-1988, a consensus was reached to undertake a review of the usefulness of seabirds as bio-indicators of changing environments. The topic was considered to be of global interest with more than 70% of respondents to the call for possible symposia titles suggesting the subject area. A decision was taken to adopt a symposium proposal submitted by Dr R.W. Furness entitled "Seabirds as monitors of changing marine environments" with Dr Furness and Dr D.N. Nettleship as conveners. The emphasis is on seabird and fishery interactions with the intent of assessing the potential use of marine birds (direct and indirect) as indicators of fish stock status in a variety of marine ecosystems.

Technological Innovations Workshop

Efforts by members of the Technological innovations and Seabirds-at-sea working groups resulted in the formulation of a workshop to review recent technological advancements in examining activity budgets of seabirds. Dr G.W. Gabrielsen, of the Norwegian Polar Research Institute/Norwegian Institute of Nature Research, accepted the committee's invitation to serve as chairman of the workshop. Between 1988-1990, Dr Gabrielsen and his co-chairman, Dr K.L. Kooyman, assembled an impressive group of scientists from eight countries that will meet at the 20th Congress to identify and display new measuring devices, and discuss parameters of measurement, the need for standardization of methodologies, and the interpretation of physiological function.

Other Special Interest Congress-related Initiatives

There have been a number of actions taken by the standing committee to enhance information exchange and the standardization and integration of approaches taken in various seabird research areas. Calls for further review on aspects of survey/census techniques and the structure and function of single-species and multi-species monitoring systems are high, and advancements in cooperative approaches to problem solving have been made. For example, there is now good liaison between eastern and western Atlantic and eastern Pacific, including northern regions of Norway (Svalbard), Denmark (Greenland), Canada and USA (Alaska). Two special interest groups have formed since 1986 and will meet at the 20th Congress to further discuss and review cooperative monitoring programs ("Cooperative seabird studies in the North Atlantic") and the need for computerized seabird colony databases ("Computerized colony registers - their design and use in seabird research, management and conservation"). The agenda for the SCCSR Open Meeting is robust, comprising numerous topics for discussion put forth by the seabird research community at large. Those discussions should culminate in the development of resolutions and action plans that will facilitate a more effective seabird research effort worldwide.

Bibliographies

Two major bibliographic undertakings were discussed in 1986: (1) petrel bibliography - review of progress in a comprehensive collection of citations on the biology of the Procellariidae (shearwaters and petrels) and Hydrobatidae (storm-petrels) [compiler: Dr J. Warham], and (2) initiation of the compilation of materials on the pelagic distribution and ecology of seabirds [principal compiler: Dr R.G.B. Brown]. The petrel bibliography now contains about 6,000 citations, with an expected total of about 8,000 entries. Dr Warham will be making a formal report at the SCCSR open meeting in December 1990, and may also give a demonstration of how this computerized bibliography is searched. The pelagic distribution and ecology bibliography has been advanced to an incomplete rough-working stage, comprising about 2,000 entries concentrated on work in the northern hemisphere; its present status is "inactive", but work is expected to resume early in 1991.

Nomenclature

Discussions on current issues related to seabird nomenclature and systematics by members of the SCCSR Nomenclature working group usually take place either at specialist Round Table Discussions or in association with the Standing Committee on Ornithological Nomenclature. No progress report has been received from the SCCSR working group chairman, Dr P. Devillers, although an oral report is expected to be presented at the 20th Congress SCCSR open meeting followed by a written submission.

Discussions of proposals for action have been on-going throughout the review period involving committee members and a broad cross-section of other seabird scientists from many nations. Questions of work priorities predominated, focussing on the need to bring certain information from seabird organisations, regional groups, and individual researchers together to permit unified action on specific problems and issues. Initiatives proposed by the standing committee since 1986, several of which have already been actioned or are under careful consideration, include:

Seabird conservation - there is a need for a careful collaboration between IOC and ICBP for the development of a global strategy plan for the conservation of seabirds. (Status: under discussion).

Long-term population studies - committee members consider long-term population studies of seabird populations to be essential to a better understanding of population and community dynamics and ecological requirements of seabirds. Equally important is the provision of mechanisms to facilitate publication of these extensive life-historical researches. (Status: under discussion).

Journal publications - there is a strong consensus among committee members of the need for an international journal of marine ornithology. The long-term objective is for the establishment of one first-class global journal rather than an overabundance of secondary regional seabird journals and bulletins. The committee feels that a major effort is required to discuss the roles of the various seabird groups and their coordination. The magnitude of the task to achieve that goal is formidable. (Status: under discussion).

Population surveys and monitoring - the committee recommends the development of a global view on population surveys and monitoring with international cooperation. The approach under consideration is for the establishment of a matrix of regions worldwide, each region with a subcommittee responsible for the development of a list of work priorities and specific recommendations for the placement and initiation of regional survey/monitoring systems. The SCCSR role would be one of coordination and the preparation of a preliminary proposal. (Status: under discussion).

Seabird colony registries - the development of regional, national, and international computerized databases is considered important to seabird research and management. Access to seabird colony data is a problem that will benefit from being tackled globally, with standardization of methods and procedures derived from groups already operating colony databases. The first international meeting on seabird colony databases was organised and chaired by the SCCSR chairman as a special paper session at the joint meeting of the Colonial Waterbird Society and the Pacific Seabird Group, Washington, D.C., USA, 12-16 October 1988. Participants, representing six colony databases from four countries [Britain (2), Canada (1), Norway (1), USA (2)], made detailed presentations in the program entitled "Computerized colony registries: their design and use in waterbird research, management and conservation" as a first step in the coordination of systems development. A second meeting is being held at the 20th Congress (see above). (Status: on going).

Commercial fisheries - review existing knowledge of the impact of competition for food with fisheries (which is at best fragmented and imperfect) in an attempt to identify information gaps and approaches that might be taken to correct them. The overall objective is to develop an agenda for cooperative international research efforts. (Status: under discussion).

Seabirds as bio-indicators - several investigators and research groups are addressing questions relating to the use of bird populations as indicators of environmental change. Several committee members are key coordinators of research activity within this subject area: measurement of certain parameters in population status and reproductive performance. The standing committee serves an important communication and liaison function. (Status: on going).

Population differentiation and quantitative characters - the committee feels that there is a strong need to identify the extent to which natural populations of seabirds mix with

one another and to determine the structure of populations in genetic terms. A recommendation is before the committee to set up a working group of interested parties to discuss and develop ideas of how best to tackle these questions. (Status: under discussion).

Climate change and seabirds - require the formulation of a workshop to assess the implications of climate change on populations of seabirds. (Status: in progress).

Bibliographies - develop an agenda for the preparation of additional reviews on certain species, families, and specific subjects. (Status: in progress).

The central task of the standing committee continues to be the difficulty in maintaining long-term communication and cooperation between members and their working groups, and seabird researchers at large. The exchange of information function of the committee has been largely successful, as has its role in the identification of subjects for special interest symposia and workshops on seabirds. However, it is felt that the committee's influence and effectiveness can only be enlarged by an increase in the number of active participating members, additions that will provide a broader representation of seabird researchers throughout the world. These and other issues will be reviewed and discussed at our New Zealand meetings as we plan our activities for the next four years.

Members of the Standing Committee for the Coordination of Seabird Research for the period 1986-1990 (20th Congress) are as follows:

P.H. Becker (Germany)	G.L. Hunt (USA)
Brian D. Bell (New Zealand)	W. Hsu (China)
W.R.P. Bourne (United Kingdom)	J.R. Jehl (USA)
R.G.B. Brown (Canada)	C. Jouanin (France)
P.A. Buckley (USA)	N. Kuroda (Japan)
J. Cooper (South Africa)	J.L. Mouglin (France)
J.C. Coulson (United Kingdom)	D.N. Nettleship (Canada)
J.P. Croxall (United Kingdom)	C.J.R. Robertson (New Zealand)
P. Devillers (Belgium)	R.P. Schlatter (Chile)
A.W. Diamond (Canada)	W.R. Siegfried (South Africa)
D.C. Duffy (USA)	K. Vermeer (Canada)
P.G.H. Evans (United Kingdom)	J. Warham (New Zealand)
R.W. Furness (United Kingdom)	G. Watson (USA)
A.N. Golovkin (USSR)	V. Zubakin (USSR)

The members of the IOC-SCCSR for the period 1986-1990 were appointed by President Charles G. Sibley in 1986 with three additions made later by the committee chairman to offset the loss of members (deaths and resignations).

Respectfully submitted for the Standing Committee for the Coordination of Seabird Research.

David N. Nettleship
Chairman, SCCSR

10 November 1990

REPORT OF THE STANDING COMMITTEE ON APPLIED ORNITHOLOGY

The Standing Committee on Applied Ornithology was set up at the 19th International Ornithological Congress in Ottawa in 1986 at the suggestion of the President, the late Professor Klaus Immelmann. No precise terms of reference were given to the Committee, which was therefore left to decide for itself what the scope of its activities should be in principle and what it should try to achieve in practice.

A first short, informal meeting of the available members of the Committee was held in Ottawa. Those present included Professor Valery Ilyichev, R. Dowsett, Professor V.E. Flint, Dr M. Luniak, Dr N. Nankinov, Dr E. Rutschke, and Dr J. Temple Lang. The structure, officers, method of operation and a variety of possible activities for the Committee were discussed. It was agreed that the Committee must not duplicate the work of the existing international bodies concerned with bird conservation and applied ornithology, but should work as closely as possible with them when appropriate. The Committee would have to work primarily through scientific cooperation and exchange of information. The possibility of the Committee arranging an international conference on applied ornithology was raised.

After this informal meeting in Ottawa the members of the Committee were formally appointed by Professor Sibley, the President of the 20th International Ornithological Congress. Professor Ilyichev and Dr Russell Peterson were appointed Co-Chairmen, and Dr Vladimir Yacoby and Dr John Temple Lang were appointed Co-Secretaries. The members of the Committee were asked to say what activities they thought the Committee should undertake. A very large number of suggestions were made, and it became clear that it was necessary for the Committee to choose some areas on which to concentrate, bearing in mind that the Committee has no funds of its own and that its members are widely spread throughout the world.

The first formal meeting of the Committee was on 19 May 1987 in Kecskemet, Hungary. Present were Professor Ilyichev, Dr Peterson, Dr Bankovics, Dr Cooch, Professor Nicolai, Dr Yacoby and Dr Temple Lang. Most of the meeting was devoted to discussing possible topics for discussion at the 20th Congress, the conference of the International Council for Bird Preservation in 1990, or a suggested conference to be arranged by the Committee in the USSR. It was agreed to make a number of recommendations to the Scientific Programme Committee of the 20th Congress, including a plenary session on bird conservation; symposia on collisions and conflicts between birds and aircraft, powerlines, vehicles and lighthouses; transmission by birds of diseases to man; and population explosions of wild bird species. In addition, it was agreed to support other symposia topics to be suggested by other scientists on control of damage by birds to agriculture, and captive breeding of wild bird species.

The meeting also agreed that in general the Committee should promote discussion, research and exchange of information on practical, conservation-oriented subjects. The Committee would need to set up working groups on particular areas of study, in particular on collisions involving birds, transmission by birds of diseases, and population explosions of wild bird species.

This discussion was on the basis of a paper summarising the ideas and suggestions received by Dr Temple Lang about the priorities which the Committee might adopt for its activities. These suggestions were concerned primarily with harm done by birds to man, harm done by man to birds, and also with education, research techniques, urbanisation problems concerning birds, and human use of birds.

The second formal meeting of the Committee was held in Cambridge, England, on 29 April 1989. Present were Dr Peterson, Professor Ilyichev, Dr Alvarez Lopez, Dr Blokpoel, Dr Imboden, Dr Yacoby and Dr Temple Lang. Various topics which could be described as applied ornithology were included in the scientific programme of the 20th Congress. The recommendations of the Committee had usefully influenced the programme of the Congress. It was agreed to propose a Round Table Discussion at the 20th Congress on the future role and work of the Committee. The possibility that the Committee might arrange or sponsor a conference on applied ornithology was again discussed.

It was agreed that the future work of the Committee should concern itself with applied ornithology, understood as optimising bird-man relations. This covers both reducing damage by birds to man (broadly, economic ornithology) and damage by man to birds (conservation). It is not possible wholly to separate these, since for example collisions between birds and aircraft both damage planes and kill birds. The aim should be to minimise damage to man with the minimum killing of birds. It was agreed that the Committee should try to avoid overlapping with the work of the International Council for Bird Preservation. It was pointed out that the 19th Congress had set up the Committee to interest scientists in conservation, and to raise the standards of conservation research. It is characteristic of applied ornithology that its conclusions need to be acted on by non-ornithologists, such as airport managers, agricultural advisers etc. who do not attend the International Ornithological Congresses (so that special meetings may be needed) and who may neglect or harm birds unless informed by applied ornithologists. The Committee therefore needs to make information available to these non-ornithologist users. The Committee could gather information worldwide, arrange exchange of information, and use the conclusions of scientific ornithology for practical purposes. It was agreed that the Committee should continue after the 20th Congress.

As in the case of other IOC Standing Committees, the members of the Standing Committee on Applied Ornithology were appointed by the President of the 20th Congress until the close of that Congress. During the period of 1986 to 1990 the members of the Standing Committee on Applied Ornithology were:

Co-Chairmen:

Professor Dr Valery D. Ilyichev, Dr Russell Peterson

Co-Secretaries:

Dr John Temple Lang, Dr Vladimir E. Yacoby

Dr Humberto Alvarez-Lopez

Dr George W. Archibald

Dr Attila Bankovics

Dr Miroslava Beklova
Dr A. Bold
Dr Hans Blokpoel
Dr Donald Bruning
Dr F. Graham Cooch
Dr Stephen J. Davies
Dr Robert Dowsett
Professor Dr V.E. Flint
Dr Luc Hoffmann
Professor Dr W. Hsu
Dr S.A. Hussain
Dr Noritaka Ichida
Dr Christoph Imboden
Dr Maciej Luniak
Dr Phil Moors
Dr Dmitri Nankinov
Professor Dr Jürgen Nicolai
Professor Dr Erich Rutschke

This report is respectfully submitted on behalf of the Standing Committee on Applied Ornithology of the International Ornithological Congress.

Valery D. Ilyichev, Russell W. Peterson
Co-Chairmen, SCAO

XXI CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

INTERNATIONAL ORNITHOLOGICAL COMMITTEE 1990-1994

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PRESIDENT

Christopher M. Perrins *United Kingdom*

VICE-PRESIDENT

Svein Haftorn *Norway*

SECRETARY-GENERAL

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Walter J. Bock *USA*

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Charles G. Sibley (1986-1990) *USA*

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Jean Dorst (1970-1974) *France*

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Henri Ouellet (1982-1986) *Canada*

Valery Ilyichev (1978-1982) *USSR*

Karel H. Voous (1966-1970) *Netherlands*

Charles G. Sibley (1958-1962) *USA*

Lars von Haartman (1954-1958) *Finland*

INTERNATIONAL ORNITHOLOGICAL COMMITTEE

(* Newly elected members; ** Re-elected members; + Permanent members)

SENIOR MEMBERS

Jürgen Aschoff *Germany*
 Biswamoy Biswas *India*
 Tso-Hsin Cheng *P.R. China*
 Kai Curry-Lindahl *Sweden* (died 5/12/90)
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 Paul Géroudet *Switzerland*
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 Richard Liversidge *South Africa*
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 Helmut Sick *Brazil* (died 5/3/91)
 Ernst Sutter *Switzerland*
 George D. Vasiliu *Rumania*
 John Warham *New Zealand*

Kurt Bauer *Austria*
 André Brosset *France*
 G.R.Cunningham-van-Someren *Kenya*
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 E. Max Nicholson *United Kingdom*
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Peter J. Mundy*

THE STATUTES AND BY-LAWS OF THE INTERNATIONAL ORNITHOLOGICAL COMMITTEE

The Statutes and By-Laws of the International Ornithological Committee were originally prepared by Donald S. Farner, President of the XVII International Ornithological Congress and adopted at that Congress in Berlin, 1978. They replaced the *Règlement des Congrès Ornithologiques Internationaux* adopted at the IX International Ornithological Congress in Rouen, 1938, and all amendments passed thereafter.

STATUTES

Article I Objectives and Purposes

The International Ornithological Committee (IOC) (1) promotes international collaboration and cooperation in ornithology and (2) as it deems desirable and useful, encourages international collaboration and cooperation between ornithology and other biological sciences.

To effect these objectives and purposes the IOC sponsors and promotes International Ornithological Congresses; establishes and sponsors commissions and committees as it deems appropriate and desirable; establishes or sponsors other international ornithological activities as it deems appropriate; and functions as the Section of Ornithology of the International Union of Biological Sciences.

Article II Membership and Functions

1. Size.

The size of the membership of the IOC is determined by the Committee, but may not exceed the number specified in the By-Laws (Art. I).

2. Representation.

The members shall be representative of the international distribution of ornithologists, and the number of members from each country shall be proportional to its ornithological activity.

3. Election.

New members are elected by the IOC at a regular meeting at the International Ornithological Congress from a list of nominations prepared and presented by the Executive Committee (EC). Proposals for this list can be made by any member of the IOC; they should be in writing with adequate documentation and submitted to the President and the Secretary at least six months prior to the next congress. Election to the IOC requires a simple majority of the members present and voting.

4. Term.

The term of membership is indefinite unless the member resigns voluntarily or is

absent from regular meetings of the IOC at two consecutive congresses, which constitutes automatic resignation. Resigned members may be re-elected.

5. Meetings.

The IOC meets at least twice during each International Ornithological Congress. The quorum for transaction of business at a regular meeting consists of the members present at the meeting. A member must be in attendance at a meeting in order to cast his/her vote.

6. Duties.

The duties of the IOC are: (a) to select the site of the next congress; (b) to elect new members of the IOC; (c) to elect the President, Vice-President, Secretary and any Honorary Officers of the next congress; (d) to elect members to the EC; and (e) to take actions appropriate and necessary to carry out its stated objectives and functions (Art. I).

7. Special meetings.

The President, under extraordinary circumstances, may call a special meeting of the IOC, and is obligated to do so on receipt of a petition signed by one-quarter of the members. The date set for a special meeting must permit reasonable time for consideration of the agenda and for travel arrangements. A quorum for a special meeting is one-third of the members of the IOC. Failure to attend a special meeting shall not count toward automatic resignation (Art II:4).

8. Presiding officer.

The President presides at the meetings of the IOC.

9. Communications.

Actions of the IOC are communicated to the congress and published either in the proceedings of the congress or in some other publication, as approved by the EC.

Article III Officers

A. The President

1. Election. The President is elected by a simple majority of the members present and voting at a regular meeting of the IOC at an International Ornithological Congress and is not eligible for election to the same office in two successive congresses.
2. Term. The President holds office from the conclusion of the congress at which elected until the conclusion of the following congress.
3. Duties. The President of the IOC also serves as chair of its EC, as President of the International Ornithological Congress, and (or designates a representative) as Chair of the Section of Ornithology of the International Union of Biological Sciences. The President presides at meetings of the IOC, of its EC and of the International Ornithological Congress, and appoints committees and commissions (with the exception of the EC) of the IOC and of the congress. After

consultation with the host organisation of the forthcoming congress, the President shall appoint the Secretary-General. The President appoints the Secretary of the Section of Ornithology of the IUBS.

4. Membership in the IOC. Past Presidents are permanent members of the IOC. The immediate Past President serves ex officio as a member of the EC.

B. The Vice-President

1. Election. The Vice-President is elected, following the election of the President, by a simple majority vote of the members present and voting at a regular meeting of the IOC at an International Ornithological Congress and is not eligible for election to the same office in two successive congresses.
2. Term. The Vice-President holds office from the conclusion of the congress at which elected until the conclusion of the following congress.
3. Duties. The Vice-President of the IOC also serves as Vice-Chair of the EC.
4. Succession. The Vice-President shall serve as president of the IOC in case of the inability of the elected President in office to continue until the completion of the normal term of the President in office.

C. The Secretary-General

1. Appointment. The Secretary-General is appointed by the President (Art. III:A,3) after consultation with the host organisation of the forthcoming congress.
2. Term. The Secretary-General serves until the Secretary-General of the following International Ornithological Congress is designated.
3. Duties. The Secretary-General serves as Secretary-General and Treasurer of the congress, having all local and financial responsibilities for the preparation and running of the congress, including publication of the congress proceedings. The Secretary-General may nominate, for Presidential appointment, persons to serve in definite capacities such as treasurer and editor or on various local committees for the congress. The Secretary-General serves ex officio as a voting member of the EC.
4. Membership in the IOC. Past Secretaries-General are permanent members of the IOC. The immediate Past Secretary-General serves ex officio as a member of the EC.

D. The Secretary

1. Election. The Secretary is elected, following the election of the President and the Vice-President, by a simple majority of the members present and voting at a regular meeting of the IOC at an International Ornithological Congress, and is eligible for re-election.
2. Term. The Secretary holds office from the conclusion of the congress at which elected until the conclusion of the following congress.

3. Duties. The Secretary shall keep the records of the IOC and its EC, prepare the agenda of meetings of the IOC and EC, serve as parliamentarian at these meetings, record and distribute within two months following the congress the minutes of the IOC and the EC meetings, prepare the published communications of these meetings, deal with communications of the IOC and EC as directed by the President, and assist the President and Secretary-General in preparation of the congress. The Secretary is responsible for communicating with and assisting ornithologists of potential host countries in the preparation of invitations for future congresses. The Secretary is a member of the EC.

4. Membership in the IOC. Past Secretaries are permanent members of the IOC.

E. Honorary Officers

The IOC, or the President with the consent of the EC, may appoint honorary officers, such as Honorary Presidents and Honorary Vice-Presidents of the congress, to recognise the contributions of ornithologists and other persons to the cause of international ornithology. Honorary Presidents and Honorary Vice-Presidents are members ex officio of the IOC.

Article IV The Executive Committee

1. Membership

a. The President (Art. III:A,3), Vice-President (Art. III:B,3), the Secretary-General (Art. III:C,3), the Secretary (Art. III:D,3), the immediate Past President (Art. III:A,4), and the immediate Past Secretary-General (Art. III:C,4) of the IOC until the end of the following congress.

b. An even number of elected members, as specified by the By-Laws (Art. III). No more than one of these members may be from a single country. These members shall be elected with proper attention to an adequate international distribution in the EC.

2. Election.

Nomination and election of members of the EC shall follow election of the President, Vice-President, Secretary and any Honorary Officers. Nomination shall be proposed by the existing EC. Any member of the IOC present at the meeting may make additional nominations; if seconded, these are added to the nominations proposed by the EC. Election of members of the EC is by simple majority vote of members of the IOC present and voting. Elected members are eligible for re-election as an elected member of the EC for one additional term.

3. Term.

The EC shall serve from the conclusion of the congress at which it is elected to the conclusion of the following congress.

4. Duties.

a. During the inter-congress period, the EC acts on the behalf of the IOC.

- b. During the inter-congress period, the EC has general responsibility for the scientific policy of the IOC including the programme of the congress, as specified in the By-Laws (Art. IV:4).
- c. At meetings of the IOC at an International Ornithological Congress, the EC provides:
 - (1) Nominations for the offices of President, Vice-President, Secretary, and Honorary Officers and for the elected members of the EC;
 - (2) A recommendation concerning the host country and organisation for the ensuing congress after due consideration of all invitations;
 - (3) Nominations for new members of the IOC with due consideration of Art. II:2;
 - (4) Recommendations for re-election of members considered to have resigned because of absence from two consecutive meetings, as specified in Art. II:4;
 - (5) Advice and counsel concerning any other matters deemed to be of interest within the purview or among the responsibilities of the IOC.

Article V

Amendment of the Statutes

1. Proposal of amendment.

Proposals to amend the statutes require the signatures of at least five members of the IOC from at least three countries, and must be transmitted to the President and Secretary at least twelve months before the next International Ornithological Congress. The Secretary will distribute the proposed amendments to all members of the IOC at least four months prior to the congress. At the meeting of the IOC at the congress the EC will present its recommendation on each proposed amendment.

2. Adoption.

Adoption of an amendment by the IOC requires a two-thirds majority vote of the members present and voting. Adopted amendments become effective at the close of the congress.

Article VI

Enabling Clause

Adoption of these statutes requires a two-thirds majority vote of the members of the existing IOC present and voting at a regular meeting of the International Ornithological Congress at which they are presented, having been distributed to the members prior to that meeting. Adoption of these statutes shall replace the *Règlement des Congrès Ornithologiques Internationaux* adopted in Rouen in 1938 and all amendments passed thereafter. If adopted, these Statutes become effective immediately.

BY-LAWS

Article I

The Size of the International Ornithological Committee (IOC)

The membership of the Committee shall not be more than 140. Members over 65 years of age (Senior Members), Past Presidents, Past Secretaries-General and Past Secretaries are not counted in this limit. Members of the IOC must be residents of the country that they represent. Senior Members are permanent members of the IOC and are not subjected to the requirements of Art. II.4 of the Statutes.

Article II

Meetings of the International Ornithological Committee

1. Sufficiently prior to the regular meeting of the IOC at an International Ornithological Congress, the Secretary prepares the agenda of the meeting after consultation with the President and the Secretary-General. The Secretary-General then distributes to all members the agenda of the meeting.
2. Members are requested to inform the President and the Secretary of their intention to attend the meeting and/or resign from the Committee.
3. An agenda and information on matters to be covered shall be sent to members with the notice of any special meeting called by the President.

Article III

Membership of the Executive Committee (EC)

In addition to the officers specified in Art. IV of the Statutes, the IOC elects ten members of the EC in accordance with Art. IV:1, b of the Statutes.

Article IV

The International Ornithological Congresses

1. The frequency of congresses.
Congresses will be held at four-year intervals unless, for compelling reasons, the IOC, or the EC acting on its behalf, deems otherwise.
2. The site and time of congresses.
After consultation with the EC and the host organisation, and due consideration of the interests and convenience of the members, the site in the host country and time of the congress are fixed by the Secretary-General.
3. Membership of congresses.
Membership in an International Ornithological Congress shall be open to all ornithologists and students of avian biology without distinction as to country of origin upon payment of the stated congress fee, if any. Membership and attendance at a congress shall be in accordance with the general policies of the International Union of Biological Sciences. Any limitation on the number of active members of the congress may be

made by the Secretary-General only after consultation with and agreement by the EC. Such limitation must be clearly stated in congress announcements. In the case of limitation in the number of active members, provision must be made for associate members which may not be limited in number. Members of the IOC may not be denied a place as an active member upon payment of the congress fee.

4. The scientific programme of the congress.

After consultation with the EC and the host organisation, the President appoints the Scientific Programme Committee. This Committee consists of three or more members from the host country and members from at least three other countries. The President, Secretary-General and Secretary are members ex officio of the Scientific Programme Committee. This committee is responsible to the EC for the scientific programme of the congress.

5. The organisation of the congress.

The general organisation of, and the arrangements for, the congress are the responsibilities of the Secretary-General.

6. The proceedings of the congress.

The Secretary-General is responsible for the publication of the proceedings of the congress, and serves as editor of the proceedings or appoints an editor after obtaining concurrence from the President.

7. Finances of the congress.

The Secretary-General is the treasurer and principal officer of the congress and as such is responsible for all financial matters of the congress. In consultation with the President, the Secretary-General develops the budget and fixes congress fees. After all fiscal obligations have been absolved, any surplus funds, including any from the proceedings, are made available for inter-congress activities, including arrangements for the ensuing congress.

8. Hosting of future congresses.

- (a) Invitations from countries to host an International Ornithological Congress immediately following the next scheduled congress should be sent to the President, Secretary-General and Secretary no later than six months before the next scheduled congress.
- (b) On request, the Secretary-General and the Secretary shall provide representatives of intending host countries with a list of information required in their invitation document and with general guidelines for submitting such an invitation.

Article V

Amendment of the By-Laws

1. Proposal of amendment.

Proposals to amend the By-Laws require the signature of at least three members from at least three countries and must be transmitted to the President, Secretary-General and Secretary at least twelve months in advance of the next International Ornithological Congress. At least four months prior to the congress, the Secretary shall distribute the proposed amendments to the members of the International Ornithological

Committee. At the meeting of the IOC at the congress, the EC will present its recommendation on each proposed amendment.

2. Adoption.

Adoption of the proposed amendments to the By-Laws by the IOC requires a simple majority vote of the members present and voting. Adopted amendments become effective at the close of the congress.

3. Conflict with the Statutes.

No amendment of the By-Laws can have the effect of modification of the Statutes.

Article VI

Enabling Clause

Adoption of these By-Laws requires prior adoption of the proposed Statutes and requires a simple majority vote of the members of the existing Committee present and voting at a regular meeting of the IOC at the congress at which they are presented, having been distributed to the members prior to that meeting. Adoption of these By-Laws shall replace any existing By-Laws and regulations (formal and informal) of the IOC and of the International Ornithological Congresses. If adopted these By-Laws become effective immediately.



BUCKINGHAM PALACE.

As the human population of the world continues to increase, so the populations of most other species are made to contract and give up their habitats. The endemic birds of New Zealand have also been made to suffer in other ways. The introduction of exotic animals, most of which have either displaced native species or become predators, has caused the extinction of a number of endemic bird species and given New Zealand a disproportionately high share of the world's rare and endangered birds. This in turn has led to the added threats of poaching and the illegal trade in endangered species.

The situation would undoubtedly have been far worse but for the heroic endeavours of voluntary and professional ornithologists and conservationists in New Zealand. Their struggle is at a critical stage and I hope that the presence of the 20th International Ornithological Congress in New Zealand will bring them much needed recognition and encouragement.

Of all the wild animals of this world, birds are the most frequently seen by the human population, and any changes in the numbers of resident and migratory birds is quickly noticed and reported. Birds have therefore become the 'indicator' species for wild populations as a whole. This has given ornithology a special significance in the field of nature conservation and I know that the deliberations of this Congress will be followed with great interest by the biological research community and by the whole conservation movement.

I have no doubt that the organisers have arranged an interesting and varied program, which will be of special interest to those unfamiliar with New Zealand's unique natural history.

I send you all my very best wishes for a happy and productive meeting and I hope that you will return home with greater confidence in the knowledge that you are part of a worldwide community of dedicated enthusiasts.

A handwritten signature in black ink, appearing to be 'Philip', written in a cursive style.

PRESIDENTIAL ADDRESS

**PHYLOGENY AND CLASSIFICATION OF
BIRDS FROM DNA COMPARISONS**

CHARLES G. SIBLEY

PHYLOGENY AND CLASSIFICATION OF BIRDS FROM DNA COMPARISONS

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ABSTRACT. DNA-DNA hybridization was used to compare the single-copy nuclear DNAs of ca. 1700 species of birds, representing 167 of the 171 families in Wetmore's (1960) classification. The DNA-DNA hybridization technique provides a measure of the percentage of base-pair mismatch that has accumulated in the two lineages since the two species that are being compared last shared a common ancestor. The DNA hybridization distance measures were used to reconstruct the phylogeny of the higher categories and a new classification was derived from the phylogeny. Examples of the most interesting and/or controversial results are included herein, including the ratites, barbets and toucans, sandgrouse, pelecaniforms, tubenoses, lyrebirds and bowerbirds, vireos, starlings and mockingbirds, and nectar-feeding passerines. This paper is a synopsis of research performed at Yale University (1974-1986) with the collaboration of Dr. Jon E. Ahlquist and the assistance of many persons in the field and laboratory. A classification based on the DNA-DNA hybridization data has been published in *The Auk* (Sibley et al. 105: 409-423, 1988.) Sibley & Ahlquist (1990) present details of the technique and the complete data.

Keywords: Phylogeny, classification, DNA-DNA hybridization.

INTRODUCTION

The avian lineage branched from its reptilian ancestor in the Jurassic Period, about 150 million years ago. The ca. 9700 living species of birds may be less than 10% of the species that have existed since the origin of the group. There are few fossils of Mesozoic birds and most may not have left living descendants. Cenozoic fossils are more abundant, but bird bones are fragile and the record is sparse compared with that for other groups of vertebrates. Until the advent of molecular methods some 35 years ago, avian systematists had to rely mainly on comparative anatomy for evidence of the phylogenetic relationships among living lineages of birds. Closely related species are usually easy to recognize, but as the phylogenetic distances among taxa increase the interpretation of morphological characters becomes more difficult. For example, we can see that ducks, geese, and swans are closely related to one another, but which group is most closely related to them? This question applies to most of the higher categories of birds and during the 19th century it led to many proposals concerning the relationships among the major groups of birds. The classification of Hans Gadow (1892, 1893) became the principal basis for that of Alexander Wetmore (1930, 1960), and Erwin Stresemann (1934) presented a system based mainly on those of Gadow and Maximilian Furbringer (1888). These two classifications have been widely used for the past 60 years. The history of avian classification and evidence of the phylogeny of birds have been reviewed by Sibley & Ahlquist (1990). This paper is a synopsis of some of our proposals concerning the phylogeny and classification of birds, based on studies using the technique of DNA-DNA hybridization. Some new data are presented and some corrections are noted.

METHODS

DNA-DNA hybridization measures the degrees of genetic similarity between species. "Hybrid" double-stranded DNA molecules are formed from the single strands of the DNAs of two species. The hybrid molecules are then dissociated ("melted") in a thermal gradient under controlled conditions such that a measure of the difference between the two nucleotide sequences may be calculated. The experimental conditions are set so that only homologous sequences can form double-stranded structures. The melting temperature of a DNA duplex molecule is a function of the number of correctly base-paired nucleotides, thus it is a measure of the degree of genetic similarity between the two single strands forming the duplex. Data are expressed as melting curves and as distances between the midpoints of the melting curves. Dendrograms that do, and do not, assume equal rates of genomic evolution along all branches may be constructed to represent the branching pattern of the phylogeny indicated by the distance values. The technique, data analysis, and other aspects of the procedures are described by Sibley & Ahlquist (1983, 1986, 1987, 1990). The principal steps in the DNA-DNA hybridization technique follow:

1. Extract and purify DNA from cell nuclei = remove proteins, RNAs, etc.
2. Shear long-chain DNA strands into fragments ca. 400-600 bases in length.
3. Remove most of the copies of repeated sequences from selected species to produce "single-copy DNA."
4. "Label" the single-copy DNA with a radioactive isotope to produce a "tracer" DNA of one species = Species A.
5. Combine the single-stranded tracer DNA of Species A with the single-stranded "driver" DNA of the same species (A + A), and with the single-stranded driver DNAs of other species (A + B, A + C, A + D, etc.). Each combination is placed in a separate vial.
6. Incubate the vials in a waterbath at 60°C for 120 hours to permit the formation of double-stranded hybrid molecules composed of one strand of the tracer (A) and one strand of the driver (B, C, D, etc.) to produce the hybrids: A x A, A x B, A x C, A x D, etc.
7. Place the DNA-DNA hybrids on hydroxyapatite (HAP) columns. Double-stranded DNA binds to HAP; single-stranded DNA does *not* bind to HAP.
8. Place the columns in a heated waterbath and raise the temperature in 2.5°C increments from 55 to 95°C. At each temperature, wash off (elute) the single-stranded DNA resulting from the "melting" of the hydrogen bonds between base pairs. Collect each eluted sample in a separate vial and assay the radioactivity in each vial. This is a measure of the percentage of hybrid molecules that melted at each temperature.
9. The melting temperature of a DNA-DNA hybrid is proportional to the degree of genetic similarity between the two single strands forming the hybrid molecule. Use the amount of radioactivity in each sample to construct melting curves and to calculate genetic distance values. Construct "trees" from the genetic distance values.

In the following brief accounts of the major groups of birds, it is assumed that readers are familiar with the geographic distributions of most groups and with the English names of groups and/or species. English and scientific names follow Sibley & Monroe (1990).

In the classification of Sibley et al. (1988) the boundaries of categories are based on the DNA hybridization distance values ($\Delta T_{50}H$). For example, Orders are groups that differ from one another by an average $\Delta T_{50}H$ value between 20 and 22; Families differ by $\Delta 9-11$, etc. We use the following categories and ranges of $\Delta T_{50}H$ values: Class (31-33), Subclass (29-31), Infraclass (27-29), Parvclass (24.5-27), Superorder (22-24.5), Order (20-22), Suborder (18-20), Infraorder (15.5-18), Parvorder (13-15.5), Superfamily (11-13), Family (9-11), Subfamily (7-9), and Tribe (4.5-7).

RATITES AND TINAMOUS

The living ratites (Ostrich, rheas, Emu, cassowaries, kiwis) form a monophyletic group (Struthioniformes) with the tinamous (Tinamiformes) as their closest living relatives. The Emu and cassowaries (Casuariidae) are closely related to one another, and more closely related to the kiwis (Apterygidae) than to the Ostrich (Struthionidae) and rheas (Rheidae). The branches leading to the Ostrich, rheas, and the Emu-cassowary-kiwi cluster occurred close together, probably in the late Cretaceous. The present distribution of the ratites is a result of the breakup of Gondwanaland and the drift of the southern continents to their present positions. The ancestor of the kiwis and moas may have reached New Zealand via stepping-stone islands across the northern Tasman Sea.

GALLINACEOUS BIRDS AND WATERFOWL

The guans (Cracidae) and megapodes (Megapodiidae) are placed in a separate order (Craciformes) from the Galliformes. The New World quail (parvorder Odontophorida) are not closely related to the pheasants, Old World quail, grouse, turkeys, and guineafowl (parvorder Phasianida). The waterfowl (Anseriformes) seem to be the closest living relatives of the gallinaceous birds, but the divergence was probably in the late Cretaceous or early Tertiary.

Sibley et al. (1988) included the parvclass Galloanserae (Craciformes, Galliformes, Anseriformes) with the ratites and tinamous (parvclass Ratitae) in the infraclass Eoaves. Sibley & Ahlquist (1990: 255, 288) and Sibley & Monroe (1990: 5) moved the Galloanserae to the beginning of the infraclass Neoaves.

BUTTONQUAILS

The Turnicidae are distant from all other living groups. The Australian Plains-wanderer *Pedionomus* is not closely related to *Turnix*, but is a charadriiform related to the seedsnipe, as proposed by Olson & Steadman (1981) and supported by our DNA hybridization evidence. *Turnix* species begin to breed at less than one year of age, at least in captivity, and may have evolved at an exceptionally rapid rate. This may account, in part, for the large genetic distance between the buttonquails and other groups.

Sibley et al. (1988) placed the "Family Turnicidae" in the "Infraclass?" and in "Order Turniciformes, *inc. sedis*". Sibley & Ahlquist (1990: 255, 257) and Sibley & Monroe

(1990: 42) substituted the parvclass Turnicae for "Infraclass?" and deleted the "*inc. sedis*" after Order Turniciformes. The revised classification for this section follows.

Class Aves

- Subclass Neornithes
 - Infraclass Eoaves
 - Parvclass Ratitae
 - Infraclass Neoaves
 - Parvclass Galloanserae
 - Parvclass Turnicae
 - Order Turniciformes

WOODPECKERS, HONEYGUIDES, BARBETS, AND TOUCANS

These groups (Piciformes) produced some intriguing results. As expected, the woodpeckers and honeyguides (infraorder Picides) are closest relatives, but the toucans proved to be more closely related to the New World barbets than the New World barbets are to the Old World barbets. Thus, the toucans are specialized New World barbets, as indicated in the following classification:

- Infraorder Ramphastides
 - Superfamily Megalaimoidea: Asian Barbets
 - Superfamily Lybioidea: African Barbets
 - Superfamily Ramphastoidea
 - Family Ramphastidae
 - Subfamily Capitoninae: New World Barbets
 - Subfamily Ramphastinae: Toucans

JACAMARS AND PUFFBIRDS

The Galbuliformes often have been viewed as close relatives of the Piciformes because they share several morphological characters. The DNA evidence indicates that these two groups are related, but that the divergence between them was ancient, hence we placed them in separate, but adjacent, parvclasses. The jacamars and puffbirds seem to be more closely related to the Coraciae (hornbills, hoopoes, trogons, rollers, motmots, etc.) than to the woodpeckers, honeyguides, barbets, and toucans.

HORNBILLS, HOOPOES, TROGONS, ROLLERS, MOTMOTS, TODIES, KINGFISHERS, AND BEE-EATERS

We assigned these groups to four orders: Bucerotiformes (hornbills); Upupiformes (hoopoes); Trogoniformes (trogons), and Coraciiformes (rollers, motmots, todies, kingfishers, bee-eaters) in the superorder Bucerotimorphae. They are morphologically diverse, but the DNA evidence indicates that they are more closely related to one another than any one of the orders is to another group.

The kingfishers are morphologically similar, but the DNA comparisons revealed substantial genealogical diversity. We divided them into two parvorders (Alcedinida; Cerylida) and the Cerylida into two superfamilies, each with one family. The family name Halcyonidae has priority over Dacelonidae (W. Bock, pers. comm.), thus our classification of the kingfishers is revised as follows:

Suborder Alcedini

Parvorder Alcedinida

Family Alcedinidae: Alcedinid Kingfishers

Parvorder Cerylida

Superfamily Halcyonoidea (replaces Dacelonoidea)

Family Halcyonidae: Halcyonid Kingfishers (replaces Dacelonidae)

Superfamily Ceryloidea

Family Cerylidae: Cerylid Kingfishers

MOUSEBIRDS OR COLIES

The Mousebirds of Africa possess several unique characters and all attempts to ally them closely with another group have failed. The DNA evidence also shows that the Coliiformes have no close living relatives; they are the survivors of an ancient lineage. Their closest relatives are probably the groups that include the hornbills, rollers, kingfishers, and cuckoos.

CUCKOOS, HOATZIN, AND TURACOS

The cuckoos and turacos often have been associated in classifications but we found no convincing evidence of a close relationship between them. The cuckoos (Cuculiformes) proved to be remarkably diverse and we found it necessary to divide them into two infraorders, five parvorders, and six families — far different from the traditional assignment of all species to the Cuculidae. The cuckoos are another ancient lineage in which morphological conservatism has obscured their genealogical diversity. Their next nearest living relatives are uncertain and we cannot identify a single group with confidence. The owls and nightjars may be the nearest living relatives of the cuckoos, but the divergence must have been so long ago that the idea of “close relatives” becomes irrelevant. It seems likely that the living cuckoos are about equally distant from several of the other non-passerine groups.

The Hoatzin *Opisthocomus hoazin* occurs in northern South America and has been a taxonomic puzzle since its discovery over 200 years ago. It was usually assigned to the Galliformes, perhaps because it somewhat resembles a chachalaca. The Hoatzin feeds mainly on plants and has a large, muscular crop and other adaptations related to its diet. The DNA evidence is clear; the Hoatzin is a highly specialized cuckoo, most closely related to the Guira Cuckoo, the anis *Crotophaga*, and the roadrunners, as indicated in the following arrangement of the infraorder Crotophagides.

Parvorder Opisthocomida: Hoatzin

Parvorder Crotophagida: Anis and Guira Cuckoo

Parvorder Neomorphida: Roadrunners, Ground Cuckoos

PARROTS

Parrots are parrots. They seem to have no close living relatives and there is no doubt about what is and what is not, a parrot. They are the descendants of an ancient lineage that has maintained the characteristic structures of beak, feet, and plumage. Our limited data do not provide the basis for subdivisions of the Psittacidae, but it seems likely that such subunits exist, possibly in relation to major geographic regions of the world.

SWIFTS AND HUMMINGBIRDS

The swifts and hummingbirds have been associated in most classifications of the past 150 years. Our DNA comparisons, and morphological evidence, indicate that they are one another's closest living relatives, but the divergence was ancient, possibly in the late Cretaceous.

OWLS, NIGHTJARS, AND ALLIES (STRIGIFORMES)

The owls and nightjars usually have been thought to be related and the DNA comparisons agree, but the divergence was a long time ago. The owls and diurnal raptors (Falconiformes) are not closely related. The next nearest relatives of the Strigiformes may be the swifts and hummingbirds, but the evidence is not conclusive.

The "nightjars and allies" include the owlet-nightjars, frogmouths, Oilbird, potoos, eared-nightjars, nighthawks, and whip-poor-wills. We recognize two suborders in the Strigiformes for the nightjars and, allies: Aegotheli for the owlet-nightjars (*Aegotheles*) and Caprimulgi for the others. Thus, contrary to most classifications, the DNA comparisons indicate that the owlet-nightjars and frogmouths are not close relatives, although both occur in Australasia. The frogmouths are separated as the infraorder Podargides from the remainder of the Caprimulgi (infraorder Caprimulgides). The South American Oilbird (*Steatornis*) is most closely related to the Neotropical potoos (*Nyctibius*). The eared-nightjars (*Eurostopodus*) are distinct from the typical nightjars and we place them in the Eurostopodoidea as the sister taxon of the Caprimulgoidea, which includes the typical nightjars, nighthawks, and whip-poor-wills.

Thus, like the parrots and kingfishers, the nightjars and allies have retained a similar external morphology while diverging substantially at the genomic level. Their plumage coloration is obviously correlated with their crepuscular and nocturnal habits, but it also obscures their diversity.

PIGEONS AND DOVES

Pigeons and doves occur on all continents and many islands. They share a common morphology and the group is certainly monophyletic. Their nearest relatives have been uncertain but the sandgrouse and parrots have often been suggested. The DNA comparisons support the monophyly of the Columbiformes, but show that the sandgrouse are related to the Charadriiformes and that the parrots are no closer to

the pigeons than to other groups. Thus, the Columbiformes seem to have no close living relatives.

CRANES, BUSTARDS, SUNGREBES, TRUMPETERS, RAILS, AND ALLIES

The Gruiformes are morphologically diverse and it would not have been surprising if the DNA comparisons had revealed at least equal degrees of genomic diversity, but the monophyly of most of the traditional members of the order is reflected in the data, although the differences among the subgroups are substantial. Two genera often included in the Gruiformes were misplaced there. The buttonquails (Turnicidae) are not members of this order; we have assigned them to the Turniciformes, noted above. The Plains-wanderer (*Pedionomus*) of Australia was transferred to the Charadriiformes by Olson & Steadman (1981) and the DNA data agree. The buttonquails and the Plains-wanderer were usually included as the only members of the Turnicidae in the traditional Gruiformes.

The DNA evidence indicates that the Limpkin (*Aramus*) and the Neotropical Sungrebe (*Heliornis*) are closest relatives. The DNAs of the African and Asian finfoots were not available.

SHOREBIRDS: SANDGROUSE, SANDPIPERS, PLOVERS, GULLS, ETC.

In our classification the suborder Charadrii includes the traditional charadriiforms in the infraorder Charadriides and the sandgrouse in the infraorder Pteroclidides. The classification of the subgroups in the Charadriides was modified by the DNA evidence, but is congruent with other sources of evidence. We divide the Charadriides into the parvorders Scolopacida (seedsnipe, Plains-wanderer, snipe, sandpipers, phalaropes, painted-snipe, jacanas) and Charadriida (thick-knees, oystercatchers, avocets, stilts, plovers, Crab Plover, pratincoles, skuas, skimmers, gulls, terns, auks).

The sandgrouse (Pteroclididae) have been the subject of a long debate; are they pigeons or plovers? Sandgrouse occur in arid regions in Africa, southern Europe, and parts of Asia. The pigeons, plovers, and galliforms most often have been proposed as their closest relatives. The relationship to the shorebirds seems clear, but the divergence was ancient and the morphological characters provide the basis for arguments in favor of both pigeons and plovers as closest relatives. Sibley & Ahlquist (1990: 463-470) reviewed the history of the debate and the evidence for and against each hypothesis. Another debate involving the sandgrouse concerned the early report that the adults transport water to their nestlings by wetting the breast feathers from which the young birds suck the water (Meade-Waldo 1896). This was dismissed by several authors, but confirmed by Cade & Maclean (1967) who observed and filmed adult male sandgrouse transporting water in their specialized ventral feathers.

HAWKS, EAGLES, OLD WORLD VULTURES, FALCONS, AND ALLIES

The diurnal birds of prey provide ample material for debate and conjecture. Are the owls closely related to the hawks? Are the falcons closely related to the hawks? What are the relationships of the Secretary-bird, the Osprey, and the New World vultures? We concluded that (1) the owls are not closely related to the hawks; (2) the

Secretary-bird and the Osprey are members of the parvorder Accipitrada, which includes the hawks, eagles, and Old World vultures; (3) the falcons are members of the parvorder Falconida, the sister group of the Accipitrada; and (4) the New World vultures are most closely related to the storks, as suggested by Garrod (1873) and supported by Ligon (1967). In effect, the New World vultures are carrion-eating storks.

GREBES

Most classifications have viewed grebes and loons as closest relatives, although they differ in many morphological characters and their similarities have been ascribed to convergence by some authors. The problem has been to identify the nearest relatives of each if they are not considered to be one another's closest relatives. The DNA comparisons show that the grebes have no close living relatives and that the grebe lineage branched early from a common ancestry with several other groups in the order Ciconiiformes, suborder Ciconii, infraorder Ciconiides. The Ciconiides includes the grebes, tropicbirds, boobies, cormorants, herons, flamingos, New World vultures, storks, ibises, Shoebill, pelicans, frigatebirds, penguins, loons, and tubenoses. Within this assemblage the loons are most closely related to the penguins and tubenoses, as noted below under Albatrosses, Petrels, Penguins, Loons, and Frigatebirds. Thus, the loons are no closer to the grebes than are the members of several other groups of waterbirds.

THE TOTIPALMATE SWIMMERS: TRADITIONAL ORDER PELECANIFORMES

The traditional Pelecaniformes includes the pelicans, boobies, gannets, cormorants, anhingas, frigatebirds, and tropicbirds. These groups share several morphological characters, including the totipalmate foot, intraorbital salt gland, and lack of a brood patch. All but the tropicbirds have an obvious gular pouch, although that of the frigatebirds is of uncertain homology. The monophyly of the "Pelecaniformes" has seemed to be beyond doubt, but the DNA comparisons indicate (1) that the boobies, gannets, anhingas, and cormorants are closely related to one another; (2) that the tropicbirds are distant from the other pelecaniforms; (3) that the frigatebirds are most closely related to the tubenoses, penguins, and loons, and (4) that the pelicans are closest to the Shoebill *Balaeniceps rex*. Many ornithologists will reject at least some of these suggestions, but there is congruent evidence. Several studies have concluded that the tropicbirds and frigatebirds are the most distant from one another and from the pelicans, boobies, gannets, anhingas, and cormorants. An alliance between frigatebirds and tubenoses has been proposed before, and the Shoebill-pelican relationship was suggested by Cottam (1957) from an anatomical study. This may be the most controversial question we have raised, but the polyphyly of the traditional order Pelecaniformes should be considered as an alternative hypothesis to be tested by independent studies of molecules and morphology.

HERONS, FLAMINGOS, IBISES, STORKS, AND ALLIES

The long-legged, long-necked wading birds usually have been placed in the order Ciconiiformes. In our classification they are members of the parvorder Ciconiida (in

the Ciconiiformes) which also includes the pelicans, New World vultures, frigatebirds, penguins, loons, and tubenoses (Procellariidae). The other members of the Ciconiida are the herons, Hamerkop (*Scopus*), flamingos, ibises, spoonbills, Shoebill, and storks. Most of these groups will elicit no surprise, but we have been accustomed to finding the tubenoses and penguins together at the beginning of the series of non-passerine groups where, in our classification, now reside the woodpeckers, barbets, rollers, and their allies. This suggests that, except for the anseriforms, the oldest volant non-passerines were terrestrial birds, not waterbirds.

We concluded (Sibley & Ahlquist 1990: 527) that "the herons, Hamerkop, flamingos, ibises, Shoebill, pelicans, New World vultures, and storks are more closely related to one another than any one of them is to another group." However, we noted the complications introduced by different ages at first breeding and the correlated differences in average genomic rates of evolution. We are not satisfied that our data are without error and additional experiments should be devised to test our conclusions. The final word, if ever uttered, is certain to be instructive.

ALBATROSSES, PETRELS, PENGUINS, LOONS, AND FRIGATEBIRDS

A relationship between the tubenoses (our Procellariidae = traditional Procellariiformes) and the penguins has long been accepted. The loons have sometimes been placed with, or near, the tubenoses, and the frigatebirds share several morphological characters with petrels. These groups also differ and the large albatrosses are among the taxa with the greatest ages at first breeding. Members of some populations of the Wandering Albatross may not breed until 15 years old, but most albatrosses begin to breed between 6 and 12 years of age. The effect of delayed maturity is to cause a slower rate of accession and drift of neutral alleles which constitute a substantial percentage of the genome and therefore have a major effect on the average rate of genomic evolution. This subject is discussed by Sibley & Ahlquist (1990: 165-183).

We concluded that the tubenoses, penguins, loons, and probably the frigatebirds are more closely related to one another than any one of them is to another group. We also noted that the relationships of the frigatebirds require further study and that the different average rates of genomic evolution among members of these groups complicate the interpretation of the data.

The major groups in our classification of the Order Ciconiiformes are as follows:

Order Ciconiiformes

Suborder Charadrii: sandgrouse and traditional Charadriiformes.

Suborder Ciconii

Infraorder Falconides: Osprey, hawks, Secretary-bird, Old World vultures, falcons.

Infraorder Ciconiides

Parvorder Podicipedida: grebes.

Parvorder Phaethontida: tropicbirds.

Parvorder Sulida: boobies, gannets, anhingas, cormorants.

Parvorder Ciconiida

Superfamily Ardeoidea: herons, bitterns, egrets.

Superfamily Scopoidea: Hamerkop or Hammerhead.

Superfamily Phoenicopteroidea: flamingos.

Superfamily Threskiornithoidea: ibises, spoonbills.

Superfamily Pelecanoidea: Shoebill, pelicans.

Superfamily Ciconioidea: New World vultures, storks.

Superfamily Procellarioidea: frigatebirds, penguins, loons, petrels, albatrosses.

ORDER PASSERIFORMES: THE PASSERINE BIRDS

This order includes 5712 (59%) of the 9672 species recognized by Sibley & Monroe (1990). Most species begin to breed at the age of one or two years and we have detected little or no effect on relative rates of genomic evolution of different ages at first breeding. The suboscine passerines (suborder Tyranni) are characterized by syringeal and other characters and the DNA data delineate essentially the same groups defined by morphology.

The oscine passerines (suborder Passeri) were treated by Wetmore (1960) and other systematists as a linear series of families with little or no structure in the form of superfamilies and subfamilies. In most cases, superficial similarities were used to classify the oscines and the classifications concealed the genealogical diversity, adaptive radiations, and other aspects of the evolution of the group. The DNA hybridization comparisons revealed a different picture of passerine phylogeny and provided the basis for a new classification. Perhaps the most interesting aspect of our phylogeny and classification is the recognition of the Australo-Papuan endemic radiation and its effects in other parts of the world.

OLD WORLD SUBOSCINES

New Zealand Wrens (Acanthisittidae). The acanthisittids seem to be the survivors of an ancient lineage with no close living relatives. We include them in the Tyranni because they are not oscines. We place them in the infraorder Acanthisittides, but it is possible that they should be assigned to a third suborder.

Pittas (Pittidae) and Broadbills (Eurylaimidae). The pittas and broadbills are placed in the infraorder Eurylaimides. We lacked DNAs of the philepittids of Madagascar.

NEW WORLD SUBOSCINES

The DNA comparisons show that the New World suboscines (infraorder Tyrannides) are more closely related to one another than any one of them is to any of the Old World suboscines. This agrees with some other studies and disagrees with the Wetmore (1960) classification.

Tyrant Flycatchers and allies (Tyrannidae). In this group we include the typical tyrants (Tyranninae), mionectine flycatchers (Pipromorphinae), tityras and becards (Tityrinae),

cotingas (Cotinginae), and manakins (Piprinae). The Pipromorphinae has been substituted for "Mionectinae" and "Corythopinae" for a group of tyrants delineated by the DNA comparisons. Lanyon (1988) rejected our separation of the pipromorphine genera because syringeal characters are not congruent with the boundaries we set. There are other controversies concerning the details within the Tyrannida which are discussed by Sibley & Ahlquist (1990: 590-597). We conclude that the Tyrannidae, as defined above, is a monophyletic cluster representing an adaptive radiation composed primarily of insectivores and frugivores.

The Neotropical antbirds were shown to be composed of two groups (typical antbirds and ground antbirds) on the basis of sternal notches (Heimerdinger & Ames 1967) and syringeal characters (Ames 1971). The DNA data delineated the same clusters and also revealed that the typical antbirds (Thamnophilidae) may be separated in the parvorder Thamnophilida, distinct from the Furnariida which includes the ovenbirds, woodcreepers, ground antbirds, gnateaters, and tapaculos.

The New World suboscines are the descendants of an adaptive radiation that occurred while South America was isolated from other continents during the Tertiary.

OSCINES OR SONGBIRDS: SUBORDER PASSERI (PASSERES)

The complex syringeal musculature and other characters define the Passeri. In our classification the Passeri contains 4561 species in 870 genera, thus by far the largest suborder of living birds. The DNA hybridization data made it possible to subdivide this group into two parvorders, each composed of three superfamilies, and to recognize 35 (or 36) families. Other classifications have usually recognized more families (36-91), but several of our subfamilies are equivalent in content to the families of other classifications. Our classification of the oscines follows. Tribes are not indicated. Changes from Sibley et al. (1988) are indicated by an asterisk*.

Parvorder Corvida

Superfamily Menuroidea

Family Climacteridae: Australo-Papuan tree-creepers.

Family Menuridae

Subfamily Menurinae: lyrebirds.

Subfamily Atrichornithinae: scrub-birds.

Family Ptilonorhynchidae: bowerbirds.

Superfamily Meliphagoidea

Family Maluridae

Subfamily Malurinae: fairywrens, emuwrens.

Subfamily Amytornithinae: grasswrens.

Family Meliphagidae: honeyeaters.

Family Pardalotidae

Subfamily Pardalotinae: pardalotes.

Subfamily Dasyornithinae: bristlebirds.

Subfamily Acanthizinae: scrubwrens, thornbills, whitefaces.

Superfamily Corvoidea

*Family Petroicidae: Australo-Papuan robins. (Bock 1990: 629 notes that Petroicidae, not Eopsaltriidae, is the correct name for this group.)

Family Irenidae: fairy-bluebirds, leafbirds.

Family Orthonychidae: Logrunner, Chowchilla.

Family Pomatostomidae: Australo-Papuan babblers.

Family Laniidae: true shrikes = *Lanius*, *Corvinella*, *Eurocephalus*.

Family Vireonidae: vireos, greenlets, peppershrikes, shrike-vireos.

Family Corvidae

Subfamily Cinclosomatinae: quail-thrushes, whipbirds.

Subfamily Corcoracinae: White-winged Chough, Apostlebird.

Subfamily Pachycephalinae: sittellas, *Mohoua* (incl. *Finschia*), shrike-tits, *Oreoica*, *Rhagologus*, whistlers, shrike-thrushes.

Subfamily Corvinae: crows, jays, magpies, birds-of-paradise, *Melampitta*, currawongs, wood-swallows, Bornean Bristlehead, *Peltops*, orioles, cuckoo-shrikes.

Subfamily Dicrurinae: fantails, drongos, monarchs, magpie-larks.

Subfamily Aegithininae: ioras.

Subfamily Malaconotinae: bushshrikes, helmetshrikes, *Batis*, *Platysteira*, vantas.

Family Callaeatidae *inc. sedis*: New Zealand wattlebirds.

*Family Picathartidae *inc. sedis*: *Picathartes*, *Chaetops*. (Sibley & Ahlquist 1990: 625).

Parvorder Passerida

Superfamily Muscicapoidea

Family Bombycillidae: waxwings, silky flycatchers, Palm Chat.

Family Cinclidae: dippers.

Family Muscicapidae

Subfamily Turdinae: thrushes.

Subfamily Muscicapinae: Old World flycatchers, chats (*Erithacus*, *Saxicola*, et al.).

Family Sturnidae: starlings, mynas, mockingbirds, thrashers, American catbirds.

Superfamily Sylvioidea

Family Sittidae

Subfamily Sittinae: nuthatches.

*Subfamily Tichodrominae: Wallcreeper. (Not Tichodromadinae).

Family Certhiidae

Subfamily Certhiinae: tree-creepers, Spotted Creeper (*Salpornis*).

Subfamily Troglodytinae: wrens.

Subfamily Polioptilinae: gnatcatchers, gnatwrens, Verdin.

Family Paridae

Subfamily Remizinae: penduline-tits.

Subfamily Parinae: titmice, chickadees.

Family Aegithalidae: long-tailed tits, bushtits.

Family Hirundinidae

Subfamily Pseudochelidoninae: river-martins.

Subfamily Hirundininae: swallows, martins.

Family Regulidae: kinglets, goldcrests.

Family Pycnonotidae: bulbuls, greenbulbs.

Family Hypocoliidae: Grey Hypocolius (*inc. sedis*).

Family Cisticolidae: African warblers (*Cisticola*, *Prinia*, *Apalis*, *Camaroptera*, et al.).

Family Zosteropidae: white-eyes, silvereyes, *Cleptornis*).

Family Sylviidae

*Subfamily Acrocephalinae: leaf warblers. (Phylloscopinae of Sibley et al. 1988).

Subfamily Megalurinae: grass warblers, incl. "*Bowdleria*" = *Megalurus*.

Subfamily Garrulacinae: *Garrulax*.

Subfamily Sylviinae: babblers, Wrentit, *Sylvia*.

Superfamily Passeroidea

Family Alaudidae: larks.

Family Nectariniidae

Subfamily Promeropinae: African sugarbirds.

Subfamily Nectariniinae: flowerpeckers, sunbirds, spiderhunters.

Family Melanocharitidae: *Melanocharis* berrypeckers, longbills.

Family Paramythiidae: Crested Berrypecker, Tit Berrypecker.

Family Passeridae

Subfamily Passerinae: sparrows, *Petronia*, snowfinches.

Subfamily Motacillinae: wagtails, pipits.

Subfamily Prunellinae: accentors, Dunnock.

Subfamily Ploceinae: weaverbirds.

Subfamily Estrildinae: waxbills, indigobirds, whydahs.

Family Fringillidae

Subfamily Peucedraminae: Olive Warbler.

Subfamily Fringillinae: chaffinches, goldfinches, crossbills, Hawaiian honeycreepers.

Subfamily Emberizinae: buntings, longspurs, towhees, wood warblers, tanagers (incl. Neotropical honeycreepers, Swallow-Tanager, Plushcap, tanager-finches), cardinals, troupials, American blackbirds, et al.

DISCUSSION

Most of the Corvoidea occur only or mainly in Australia and/or New Guinea. The exceptions are the Irenidae, Laniidae, Vireonidae, crows, jays, magpies, orioles, cuckooshrikes, drongos, monarchs, ioras, bushshrikes, helmetshrikes, *Batis*, *Platysteira*, and the vangas. Most species of wood-swallows are endemic to Australia and New Guinea, but some species occur in southern and southeastern Asia, and on Southwest Pacific islands. *Mohoua* and *Finschia* are endemic to New Zealand; whistlers and honeyeaters occur on many South Pacific islands.

The bowerbirds and the birds-of-paradise usually have been treated as closely related groups, sometimes placed in the same family or subfamily. The DNA hybridization comparisons show that the bowerbirds are closest to the lyrebirds and scrub-birds (Menuroidea); the birds-of-paradise are closest to the currawongs, orioles, and corvines (Corvoidea).

The division of the Passeri into the Corvida and Passerida is correlated with the morphology of the head of the humerus. In the Corvida the tricipital fossa is single and pneumatic, that is, there is an opening from the fossa into the hollow shaft of the humerus that forms a connection from the air sac system. About 90% of the species of the Passerida have two fossae and there is no opening into the shaft of the humerus. A few species (waxwings, for example) are intermediate between the two

extremes. These conditions are randomly distributed in relation to the Wetmore (1960) classification. This subject is discussed by Sibley & Ahlquist (1990: 571, 626, 629, 633, 639).

The African genera *Picathartes* (rockfowl) and *Chaetops* (rock-jumpers) have corvoid humeral fossae and the DNA hybridization evidence suggests that they may be closest relatives. Sibley & Ahlquist (1990: 625-627) placed the Picathartidae in the limbo of *inc. sedis* because our comparisons were incomplete.

The Corvoidea includes a disproportionate number of species that are co-operative (or communal) breeders. Russell (1989) noted that 68 co-operative breeding species occur in Australia, of which 58 are passerines. All belong to the old endemic families of the corvoid early Australian radiation. Thus, of 258 species of old endemics, at least 22% are co-operative breeders, compared with a world-wide incidence of ca. 3%. This correlation is only with the Sibley et al. (1988) classification; it does not hold with other classifications. Russell (1989) suggested that the relationship between Australian endemics and co-operative breeding evolved as a response to climatic and other environmental influences that favored this pattern of reproduction. The old endemics of Australia also tend to lay smaller clutches and to live longer than passerines in other parts of the world.

A comparison between the groups in our classification and the families of Wetmore's (1960) classification reveals many differences, including the treatment of the nectarivorous oscines. In Wetmore's classification, the honeyeaters, sunbirds, flowerpeckers, and white-eyes were listed in sequence. Wetmore viewed the sequence of groups as being on a scale of increasing specialization from the larks and swallows at the beginning of the series of oscine families to the New World nine-primaried groups at the end. By placing the nectarivorous families in sequence he implied a closer relationship among them. The DNA hybridization evidence has shown that the meliphagids are corvoids, the nectariniids are passeroids, and the zosteropids are sylvioids. The Dicaeidae of Wetmore (and others) included the pardalotes of Australia and the flowerpeckers. The DNA hybridization comparisons show that the pardalotes are corvoids and the flowerpeckers are nectariniids, hence passeroids.

The African sugarbirds (*Promerops*) have been assigned to several groups, including the Meliphagidae, Nectariniidae, Sturnidae, and Turdidae. The DNA comparisons show that the sugarbirds are specialized sunbirds and we place them in the Promeropinae of the Nectariniidae.

The vireonids usually have been placed near the nine-primaried wood warblers (Emberizinae: Parulini) because they are small, greenish or yellowish insectivores with a tendency to have a reduced 10th primary. The DNA evidence allies them with the Australian endemics in the Corvoidea. The ancestral vireonid may have arrived in South America via Antarctica when Antarctica had a temperate climate.

The starlings have been allied with the corvines in many classifications. Wetmore placed them between the New Zealand wattlebirds and the honeyeaters. The DNA comparisons showed that the starlings are most closely related to the New World mockingbirds and thrashers ("Mimidae") and we have included these groups as tribes (Sturnini, Mimini) in the family Sturnidae. This conclusion has been one of the most

difficult for many ornithologists to accept, but it is based on some of the best data in our study and it is supported by serological and morphological evidence. In addition, starlings and muscicapids are the only oscines that lack the enzyme sucrase (Martinez del Rio 1990).

The several types of "creepers" often have been placed together. Wetmore included the Northern creepers (*Certhia*) and Australo-Papuan treecreepers (*Climacteris*, *Cormobates*) in the Certhiidae, but the DNA data show that the Climacteridae is a menuroid group and *Certhia* is a sylvioid genus most closely related to the wrens, gnatcatchers, gnatwrens, and Verdin.

In some classifications the muscicapine flycatchers, thrushes, and sylviine warblers have been placed in the same family or in adjacent families. Other classifications have included the thrushes, babblers, mockingbirds, wrens, dippers, and accentors as subfamilies in the same family. Hartert (1910) included the muscicapine flycatchers, monarchs, sylviine warblers, babblers, and thrushes in his family Muscicapidae. This arrangement, usually called the "Primitive Insect Eaters," has been adopted by several subsequent authors. Hartert's Muscicapidae was a polyphyletic assemblage that included members of both of our parvorders and most of the superfamilies in the Passeri. Some classifications have included members of all six of our oscine superfamilies in the "Muscicapidae" when the Australo-Papuan treecreepers (Climacteridae) have been included in the Certhiidae.

"The convergently similar members of the Australo-Papuan Corvida and the Afro-Eurasian Passerida have presented the most difficult problems in the classification of the muscicapoid and sylvioid Passeri. The association of superficially similar but genetically unrelated ecotypes in such polyphyletic taxa as the "Muscicapidae" of many classifications has obscured the zoogeographic and phylogenetic histories of many oscine taxa. The result is a classical example of the difficulties encountered in using morphological characters to determine the boundaries of monophyletic clusters of convergently similar species." (Sibley & Ahlquist 1990: 634).

Other examples are discussed by Sibley & Ahlquist (1990) and indicated in the classification of Sibley et al. (1988).

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PLENARY LECTURE

**AN ORNITHOLOGICAL GLIMPSE INTO
NEW ZEALAND'S PRE-HUMAN PAST**

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AN ORNITHOLOGICAL GLIMPSE INTO NEW ZEALAND'S PRE-HUMAN PAST

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ABSTRACT. Data from subfossil birds, and current and past vegetation, are used to reconstruct four lowland and coastal forest-bird systems of pre-human New Zealand. These systems had relatively simple trophic structures: 67 bird species used the forests, distributed between 10 feeding guilds; 33% of the species were flightless and 21% were nocturnal or semi-nocturnal. Feeding level, feeding mode, feeding site and foods eaten, differentiated the guilds and facilitated coexistence of species within guilds. Differences in guild composition between habitats were largely a consequence of biogeographic history. The ground herbivore, arboreal herbivore, and subsurface-feeding group of the ground insectivore guilds are considered to have no counterparts elsewhere. Some 40% or more of the bird species present originally in these systems are extinct. There are limited opportunities to partly restore some systems which, if taken, may increase chances of survival for remaining members of the avifauna.

Keywords: trophic structure, guilds, resource partitioning, forest birds, feeding behaviour, species coexistence, ecological restoration, coastal forest, competition, extinctions, flightlessness, lowland forest, moas, nocturnal activity, subfossil faunas, weights.

"The past of systems influences their present behaviour and represents an often unexplained source of variance in the relationship between current environment and current process".

Peter S. White 1990

INTRODUCTION

When humans first stepped ashore in New Zealand a thousand or more years ago, they encountered one of the most remarkable plant-animal communities in the world. The largely forested landscape was dominated by birds. The absence of mammals, apart from a few species of bat, would not have been surprising to these Polynesian people given the nature of the islands from which they sailed. What was new was the large size and abundance of flightless, herbivorous birds called moa providing a plentiful supply of food.

To an ornithologist, moas would not have been the only unusual feature of this pristine terrestrial community. Other species, some of them flying birds, were also herbivorous, an uncommon behaviour among birds, and these coexisted with various other frugivorous, nectivorous, insectivorous, omnivorous and raptorial birds. Flightlessness or reduced flight capacity was found in birds of all sizes and few species were specialist feeders. Most groups showed little radiation although rails, acanthisittid wrens, and moas were notable exceptions.

What kinds of food resources were available to these birds and how was food partitioned between species? To what extent had birds in New Zealand adopted the ecological role of mammals in plant-animal systems of the continents? Partial answers to these questions are now possible as a result of both new finds of subfossil birds and recent studies of living birds. The most detailed information relates to low-altitude environments and, since forest covered more than 80% of the land area during the few thousand years immediately preceding human arrival (McGlone 1989), this study is focused on lowland and coastal forest. Reconstructions of four examples of these forests are used as the basis for a preliminary analysis of avian trophic structure in such habitats as it might have been in pre-human times.

CHARACTERISTICS OF LOWLAND AND COASTAL FOREST IN PRE-HUMAN NEW ZEALAND

The greater part of this forest consisted of a mixture of tall long-lived southern conifers and shorter-lived hardwoods of variable height. Key characteristics of this community are summarised in Table 1.

TABLE 1 – Characteristics of New Zealand lowland conifer/hardwood forest.

Characteristic	Degree of development	References
High level of endemism in both plants and animals	Angiosperms (85%); gymnosperms (100%); ferns (45%); landbirds (34%); reptiles (100%); amphibians (100%); butterflies and moths (90%)	Godley 1975; Brownsey & Smith-Dodsworth 1989; C.J.R. Robertson 1985; Daugherty et al. 1990
Low species diversity in most plant and animal groups	c. 36 significant tree species forming canopy; seldom more than 5-10 important at any one site; forest birds (c. 67 spp); reptiles (c. 22 spp.); amphibians (7 spp.); invertebrates (unknown but beetles very diverse)	I.A.E. Atkinson (unpub); D.R. Towns (pers. comm.); Worthy 1987
Plant species predominantly evergreen	Leaves rather dark green, of medium to small size, most frequently glabrous, entire with glossy upper surface	
Canopy of long-lived small-leaved conifers without cones mixed with shorter lived hardwoods frequently overtopped by the conifers	Life span of conifers commonly 500-1000 years, sometimes >1000 years, usually 25-40 m tall. Cones replaced by fleshy arils supporting the 'seeds'. Life span of hardwoods commonly 100-450 years although some species live longer.	
Tree ferns and ground ferns	Often prominent in the understorey and on the ground, particularly in wetter environments	
Epiphytes and lianes	Prominent at all levels in the forest, particularly in wetter environments	

Smaller areas of lowland forest dominated either by southern beeches (*Nothofagus* spp.), which are of major importance in the montane zone, or kauri *Agathis australis*, which occurs in a mosaic pattern with southern conifer/hardwood forest in northern North Island are excluded. Both these forests occur with soils of low fertility.

New Zealand forests have low species diversity. Many important tree genera of Australia, such as *Eucalyptus* and *Acacia*, are not indigenous to New Zealand.

FOOD SOURCES FOR BIRDS WITHIN LOWLAND CONIFER/HARDWOOD FOREST

Woody plants

In addition to leaves and buds, up to 20% of the species present in any one site may produce nectar. There are very few species with ornithophilous flowers. Unlike the southern beech forests, production of honeydew excreted by bark inhabiting scale insects is only of minor importance in conifer/hardwood forest. Manna and lerp (Paton 1980) have not been investigated as food sources for birds in New Zealand.

Up to 60% of the species at a site may produce fleshy fruit. Fruit are commonly red in colour although significant proportions are black or white (Lee et al. 1991). Few species have large fruit with none exceeding 20 mm diameter or 40 mm length; most fruit are less than 10 mm in diameter (Lee et al. 1991). The availability of nectar and fleshy fruit varies greatly from place to place depending on species composition and natural annual fluctuations in production.

Herbaceous plants

Ferns, sedges, lilies and dicotyledonous herbs are all common in conifer/hardwood forests but most are perennial and few species appear to be of high nutrient value. Grasses, including some species of tussock grass, are less common; they may be a useful source of nutrients.

Mosses, liverworts, lichens and fungi

These groups of plants are all abundant in conifer/hardwood forest; both fungi and lichens are potential food sources for vertebrates.

Invertebrates

The invertebrate life of lowland forest was once characterised by an abundance and variety of large (> 20 mm) flightless insects occupying habitats from the forest floor up into the canopy. These included very large nocturnal wingless crickets called wetas in the Stenopelmidae (giant wetas, tree wetas and ground wetas) and Rhaphidophoridae (cave wetas). More than half the known insect fauna of New Zealand are beetles and this group was also very common in forest, particularly the flightless ground beetles and large flightless weevils. Another formerly abundant food source that may have been eaten by birds are veined slugs of the family Arthorocophoridae. These live in vegetation, decaying logs and leaf mould and may reach 150 mm in length (Burton 1962, 1963).

A key source of food for many insectivorous birds is the invertebrate life in the leaf and branch litter of the forest floor. This fauna was formerly characterised by high densities of amphipods, litter-feeding caterpillars of moths, and large (up to 20 mm width) pill millipedes (Watt 1975). Where lime was not limiting there were populations of very large (up to 100 mm diam.) carnivorous molluscs which were specialised to capture and eat large subsoil earthworms, members of an extensive annelid worm fauna that occurs in leaf mould (36 spp), topsoil (48 spp), as well as in the subsoil (Lee 1959).

Many invertebrates generally associated with the forest floor are also available to arboreal insectivores. Perched leaf litters among epiphytes and in tree cavities provide important habitat for many invertebrates such as caterpillars, ants, amphipods,

ostracods, isopods and earthworms that are otherwise associated with the forest floor (Moeed & Meads 1983).

The numbers and variety of all these groups of animals have been greatly reduced since the advent of mammalian predators in New Zealand particularly rats and mice.

Vertebrates

Evidence from cave deposits and rat-free islands indicates that skinks and geckos were originally very abundant in lowland and coastal forests (Whitaker 1973, Daugherty et al. 1990). Nocturnal and diurnal skinks were largely restricted to the ground but some geckos foraged arboreally. Tuatara (*Sphenodon* spp.) were also widespread on the mainland and may have been eaten by some bird predators. Subfossil evidence and island distribution of living species of leiopelmatid frogs suggest that these also were a potential food, particularly since they lack a free-living tadpole stage.

Three species of small nocturnal bats were originally widespread in lowland forests and roosted in caves or hollow trees (Daniel & Williams 1984, Hill & Daniel 1985). Birds themselves provided prey for raptors.

METHODS USED IN HABITAT RECONSTRUCTIONS

Habitat reconstructions were attempted for two examples each of lowland and coastal forest. These were warm temperate humid conifer/hardwood and cool temperate dry conifer/hardwood forests, and warm temperate and cool temperate coastal forests. Classification of thermal regimes follows Meurk (1984). Major plant species likely to have been present were derived from knowledge of surviving forest remnants as well as identifications of charcoal and fossil wood. In each habitat a list of the birds formerly present, both extinct and extant, was derived primarily from subfossil bone deposits accumulated in caves, sand dunes or alkaline swamps. The list includes birds considered to have made some major use of these forests even if breeding in other habitats. Additional records were derived from current distribution data (Bull et al. 1985) but several species now present in particular habitats were excluded because of evidence that they may not have been present 1000 years ago. A significant number of New Zealand birds have only established since human modification of the landscape began.

The trophic position of each species was assessed from feeding habits considered in the light of body weight which is correlated with many life history parameters (Western 1979, Peters 1983). Data on feeding habits were derived from published studies and the authors' observations. Feeding habits of extinct birds were inferred where possible from bill structure together with the feeding behaviour of related extant birds where such existed.

The observed feeding patterns of some extant species may have changed in response to altered competitive relationships following species extinctions and establishment of some introduced species. For this reason the analysis is restricted to major differences in trophic behaviour between species.

TABLE 2 – Classification of avian feeding guilds in New Zealand forest.

Food source	Feeding level	Guild ¹
Foliage, twigs	ground	ground herbivores
	arboreal	arboreal herbivores
Fruit, buds, foliage	ground	} frugivore/herbivores
	arboreal	
Nectar, honeydew, fruit	arboreal	nectivores
Invertebrates	aquatic	aquatic insectivores
	ground/subsurface	ground insectivores
	arboreal	arboreal insectivores
Vertebrates	all levels	major predators (of vertebrates)
Carrion	ground/arboreal	carrion feeders

¹Guild classification modified from Lein (1972) and Terborgh et al. (1990).

TABLE 3 – Methods of foraging by New Zealand forest-inhabiting birds.

Foraging method	Description
Grazing	Foliage cut or pulled at or near ground level.
Browsing/plucking	Plants parts, including fruit, cut or pulled from vegetation, often woody.
Crushing	Use of bill to crush seeds before ingestion.
Husking	Use of bill to husk seeds from enclosing structures or extract seeds from seed capsules.
Grinding	Use of mandible to grind fibrous foods against maxilla and extract sap or other juices.
Lapping	Use of tongue to drink nectar, honeydew or sap exudate, or pick up pollen.
Gleaning ¹	Picking up stationary food items by a standing or hopping bird.
Probing/prising ¹	Use of bill to penetrate or lift the substrate to locate concealed food.
Stripping	Use of bill to peel or strip bark to locate concealed food.
Hovering ¹	Picking up food while the bird hovers.
Snatching ¹	Food plucked from the substrate by the bird as it flies past.
Pouncing ¹	Food taken from the substrate by a bird flying from a perch.
Hawking ¹	Bird sallies into the air to catch flying prey.
Flushing	Disturbance of prey by bobbing action with whole body, rapid opening and closing of wings, spreading of tail, or vibration of foot.
Raking	Use of feet or bill to scatter loose material such as leaf litter and expose concealed food.
Gauging	Use of bill to cut linear incisions in bark to reach cambium and release sap.
Digging	Use of bill to excavate holes in decaying or live wood, or in soil, to expose concealed food.

¹After Holmes & Recher (1986).

Body weights of extant birds were taken from publications or unpublished data. The weights of extinct birds were estimated either from allometric relationships between femur dimensions and body weight or, for a very few species, assessed by comparison with similar-sized living birds (Appendix 1).

Trophic relationships were described by means of feeding guilds (Table 2), i.e. sets of birds deriving their subsistence from common pools of resources and thus co-existing in the same habitat (Terborgh & Robinson 1986). Although the guild concept is useful for comparisons, the diversity of food sources used by some birds precluded any simple analysis of avian trophic structure. Where a species used different food sources between the breeding and non-breeding season, both sources were used to determine guild position.

TABLE 4 – Stratification of feeding levels used by New Zealand forest inhabiting birds.

Feeding level	Description of level	Height zone (m)
Canopy	The uppermost storey of tree (or shrub) crowns, regardless of height, unshaded by other crowns.	5-40+
Upper understorey (Subcanopy)	Plant and foliage shaded by canopy foliage. (In taller forest only : the uppermost part of the upper understorey where such distinction is useful).	>2
		>10
Lower understorey	Plant crowns and foliage shaded by canopy foliage.	0.5-2
Ground storey	Plants with growing points < 0.5 m above ground.	variable, not necessarily always < 0.5 m
Ground	The ground surface including the litter.	0.0
Subsurface	Feeding levels below the ground surface.	variable
Aquatic	Feeding levels on or below a water surface.	variable

Unless indicated, nomenclature for bird species follows Turbott (1990) although subspecific epithets are excluded from the tables. Only major foods taken are tabulated. Foraging methods are categorised in Table 3. Classification of feeding levels (Table 4) extends the system used by Atkinson (1966a). In the guild tables, feeding levels are listed in decreasing frequency of use and emphasise feeding rather than other activities. The four habitat reconstructions of the tables correspond with those described under I-IV in the text. Where two weights are given, male weights precede those of female.

I. WARM-TEMPERATE HUMID CONIFER/HARDWOOD FOREST ON KARST TERRAIN

Site description

This region of karst landscape on limestone is south-west of Hamilton, North Island. Its western boundary lies 8 km or more inland from the west coast and to the east it is bounded by the Waitomo Caves; northern and southern limits are at Raglan and Awakino respectively (Figure 1). In these Oligocene limestones (Kear 1960), karst features are prominent with numerous broken ridges and steep bluffs separated by wide intricately gullied basins with sink-holes, underground streams and caves. Although Jurassic siltstones and Pliocene Pleistocene andesites are present in the general area, this habitat reconstruction relates to limestone and will be referred to as the "Waitomo" region.

This kind of landscape varies between 100 and 400 m altitude with a mean annual temperature of 12.5 to 15°C and annual rainfall from 2000 to 2500 mm. Soils are weakly or moderately leached central yellow-brown loams that are not particularly fertile as they have been formed from a subaerially deposited layer of andesitic volcanic ash, Mairoa Ash (Orbell 1974) overlying the limestone to depths of 1 m or more (D. Hicks, pers comm). Soil pH is 5.8 to 6.0 and both base saturation and available phosphorus are low (New Zealand Soil Bureau 1954).

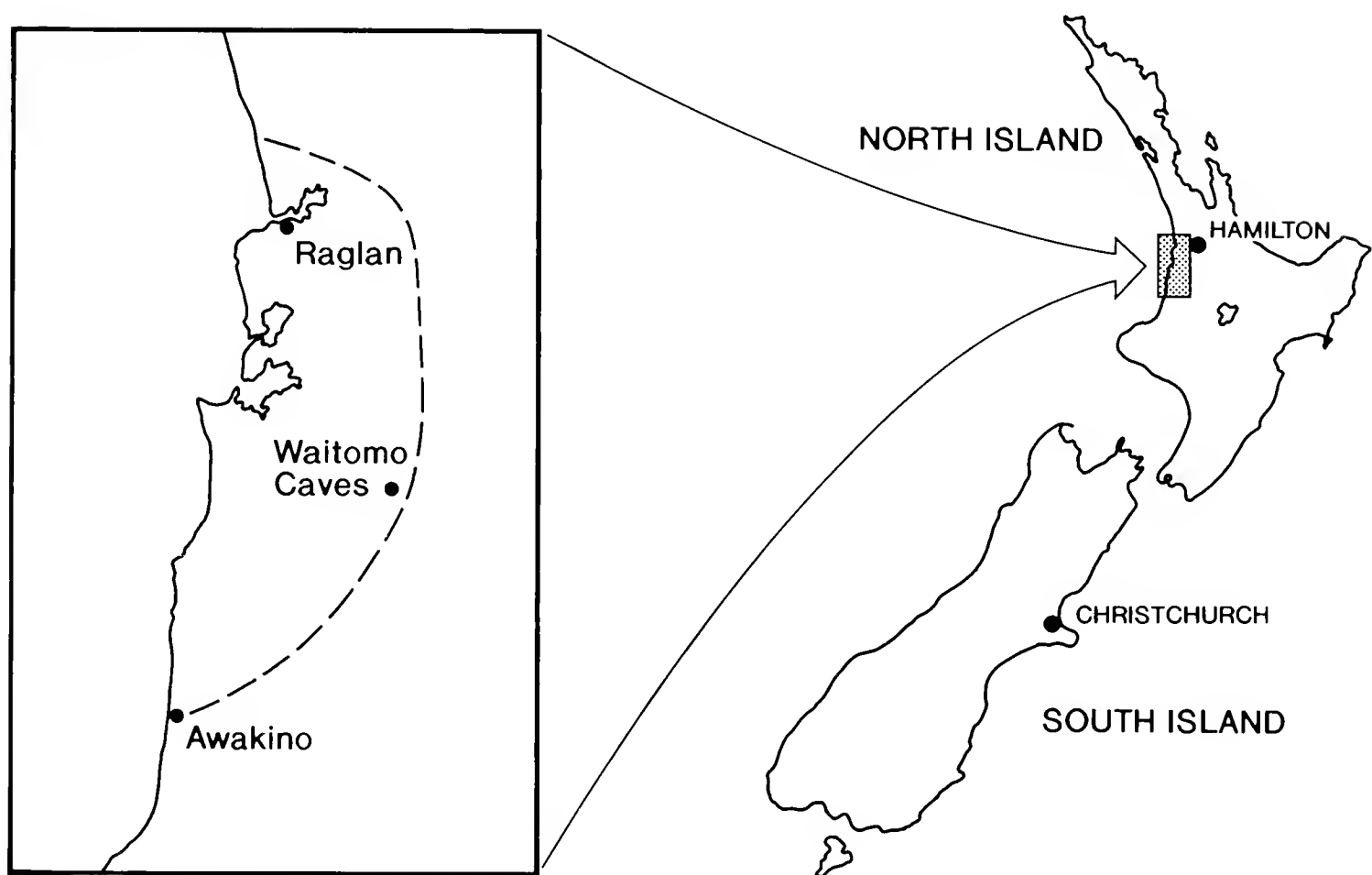


FIGURE 1 – Location of the Waitomo habitat reconstruction region.

Nature and age of the subfossil material.

The subfossil bird bones recovered are from 37 caves that together formed one of two major study areas described and analysed by Millener (1981a). These originate mainly from pitfall deposits but include some from underground stream deposits derived from larger catchments. Pitfalls may introduce a bias of unknown size towards flightless birds. The caves themselves are much older than the deposits they contain: radiocarbon dates from samples of avian bone collagen collected from 10 caves span an age range of 1075 ± 75 yr BP to $24,800 \pm 500$ yr BP.

This age range extends into Otiran time and raises the question of whether the cave-deposited bones are derived only from animals living in forest that grew in a humid warm-temperate climate? A botanical survey of parts of Tawarau Forest, immediately west of Waitomo revealed a number of “cool-climate” plant species associated with matai/kamahi¹ forest and *Olearia virgata* scrub, species that are not present in the widespread rimu/tawa forest now present in the generally mild climate of the region (Ogle & Druce 1987).

Although some caves may have been available for trapping of cool-climate animals during Otiran times, many features of the deposits demonstrate that the animals represented are those of humid forest, frequently forest associated with a warm-temperate climate. These features are:

- (i) The abundance of bones of moa species such as *Pachyornis mappini*, *Euryapteryx curtus* and *E. geranoides*, all recognised as lowland species (Atkinson & Greenwood 1989, Worthy 1990).

¹ Scientific names of plants are given in the tables.

- (ii) The common and relatively abundant bones of *Anomalopteryx didiformis*, a lowland moa which is associated with deposits of Holocene rather than Otiran age (Worthy 1990), and which was recovered from 31 of the 37 caves examined.
- (iii) The abundance of birds such as Weka, New Zealand Pigeon, Kaka, Red-crowned parakeet, Tui and Saddleback, all commonly associated with lowland forest.
- (iv) The widespread occurrence of shells of many landsnail species obligately dependent on humid forest environments.
- (v) The absence or rarity of birds such as Harrier *Circus approximans*, Pipit *Anthus n. novaeseelandiae* and New Zealand quail *Coturnix n. novaezelandiae* which would be expected in more open habitats with cool-climate vegetation.

A humid lowland forest thus dominated the area throughout the period when faunal remains were accumulating in the caves. This fauna could not have been living in scrub communities dominated by *Olearia virgata*, manuka *Leptospermum scoparium* or other species, but could have been derived in part from matai/kamahi forest of the kind described by Ogle and Druce (1987).

The dominance of lowland forest animal species in the cave deposits also suggests that most of these deposits are Holocene in age. An alternative explanation is that the area remained largely under humid forest throughout the last 25 000 years, even though pollen evidence suggests that much of the Waikato lowlands to the north-west of the Waitomo study area may have been unforested between c.18000 and 14000 yr BP (Newnham et al. 1989).

In listing the major plant and bird species for this reconstruction, we have included only those we consider to have been present in the Waitomo district throughout the period c.6000 to 1000 yr BP, whether or not they may have been present during earlier periods.

Vegetation

Rimu/tawa forest as described by Nicholls (1980) and Ogle and Druce (1987) is probably similar to the plant cover of the 6000-1000 yr BP period. This forest type covered much of the area prior to the arrival of Europeans last century. Plant species likely to have contributed the greatest proportion of biomass to the community are listed in Table 5.

The structure of the forest (Figure 2) is characterised by a three-layered canopy in which the crowns of spaced conifers, particularly rimu, and of northern rata emerge clear of the main canopy to reach heights of 40 m or more. Northern rata is more prominent on rocky outcrops above bluffs. The main canopy at 20-25 m height is composed of tawa, although kamahi is of major importance on some steeper sites subject to disturbance. Hinau, mangeao and sometimes black maire form a second discontinuous canopy layer between the discontinuous emergent layer and the semi-continuous main canopy. The understorey is relatively open and is unlikely to have impeded large birds except where supplejack was abundant. Tree ferns and ground ferns are both prominent in the understorey.

TABLE 5 – Major plant species of humid conifer/hardwood forest in the Waitomo region.

Scientific name	Common name	Abundance ¹
CANOPY AND SUBCANOPY:		
	Southern conifers	
<i>Dacrydium cupressinum</i>	rimu	c
<i>Prumnopitys ferruginea</i>	miro	c
	Hardwood trees	
<i>Beilschmiedia tawa</i>	tawa	a
<i>Elaeocarpus dentatus</i>	hinau	a
<i>Knightia excelsa</i>	rewarewa	c
<i>Laurelia novae-zealandiae</i>	pukatea	c
<i>Litsea calicaris</i>	mangeao	a
<i>Metrosideros robusta</i>	northern rata	c
<i>Nestegis cunninghamii</i>	black maire	c
<i>Quintinia serrata</i>	tawheowheo	c
<i>Weinmannia racemosa</i>	kamahi	a
	Woody lianes	
<i>Metrosideros diffusa</i>	climbing rata	a
<i>M. fulgens</i>	climbing rata	a
<i>M. perforata</i>	climbing rata	a
<i>Passiflora tetrandra</i>	NZ passion vine	c
<i>Rubus cissoides</i>	bush lawyer	a
UPPER AND LOWER UNDERSTOREY:		
	Hardwood trees and shrubs	
<i>Alseuosmia macrophylla</i>	toropapa	a
<i>Carpodetus serratus</i>	putaputaweta	c
<i>Coprosma grandifolia</i>	raurekau	c
<i>Geniostoma ruprestre</i>	hangehange	a
<i>Hedycarya arborea</i>	pigeonwood	a
<i>Melicytus ramiflorus</i>	mahoe	a
<i>Myrsine australis</i>	mapou	a
<i>Olearia rani</i>	heketara	c
<i>Pseudopanax arboreus</i>	fivefinger	a
<i>P. crassifolius</i>	lancewood	c
<i>P. laetus</i>		c
<i>Rhabdothamnus solandri</i>	waiuatua	a
<i>Streblus heterophyllus</i>	small-leaved milk tree	c
Juveniles of canopy and trees and shrubs		
	Tree ferns	
<i>Cyathea dealbata</i>	ponga	a
<i>C. medullaris</i>	mamaku	a
<i>Dicksonia squarrosa</i>	wheki	a
	Woody lianes	
<i>Freycinetia baueriana</i>	kiekie	c
<i>Griselinia lucida</i>	puka	c
<i>Metrosideros diffusa</i>	climbing rata	a
<i>M. perforata</i>	climbing rata	a
<i>Rubus cissoides</i>	bush lawyer	a
	Epiphytes	
<i>Astelia solandri</i> (lily)	astelia	a
<i>Collospermum hastatum</i> (lily)	collospermum	a
GROUND STOREY:		
	Shrubs	
<i>Coprosma rhamnoides</i>		a
<i>Gaultheria antipoda</i>	snowberry	c

TABLE 5 – (Continued)

Scientific name	Common name	Abundance ¹
Herbs, including sedges		
<i>Astelia fragrans</i>	astelia	a
<i>Gahnia pauciflora</i>	cutty grass	a
<i>Peperomia urvilleana</i>		a
<i>Uncinia uncinata</i>	hook grass	a
Ferns		
<i>Adiantum cunninghamii</i>		c
<i>Asplenium bulbiferum</i>		a
<i>A. oblongifolium</i>		a
<i>Leptopteris hymenophylloides</i>		a
<i>Phymatosorus diversifolius</i>		a

¹a = abundant species, present in 80% or more of stands
c = common species, present in 20-80% of stands

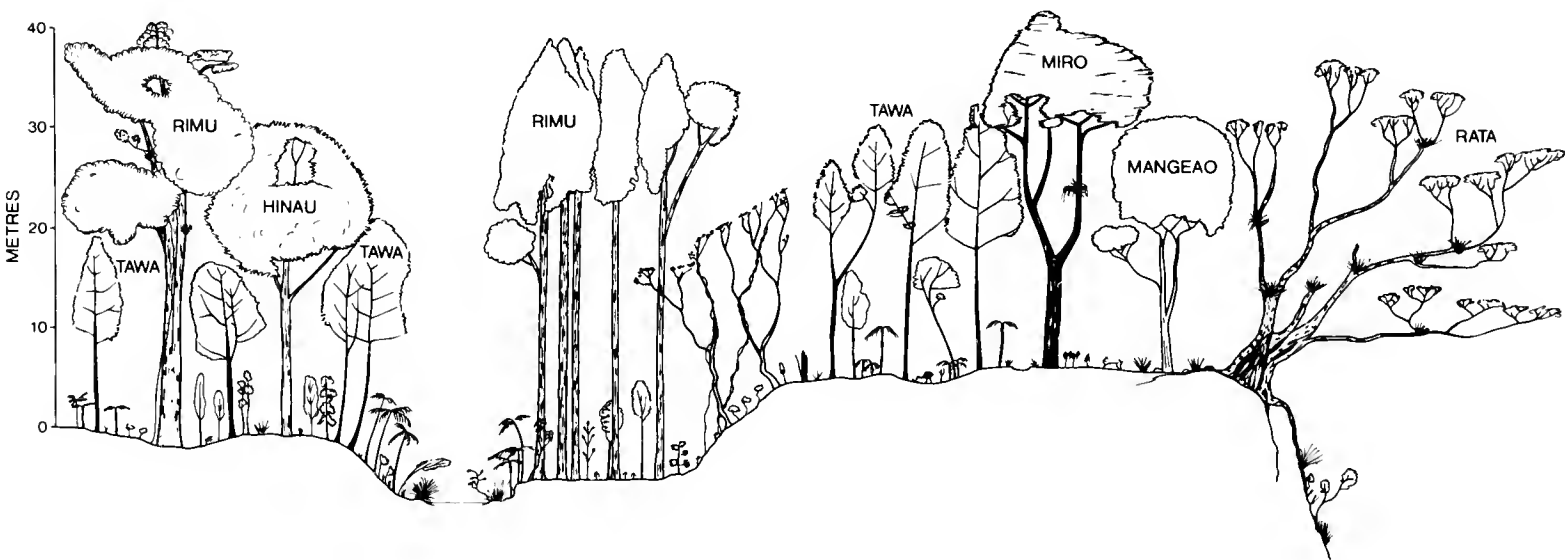


FIGURE 2 – Structure of pre-human conifer/hardwood forest in the Waitomo region. The site includes a young stand of southern conifers (rimu) on an alluvial terrace and rata growing on a limestone bluff. Scientific names of plants are given in Table 5.

Ground herbivores (Table 6, Figure 3)

Moas dominated this feeding guild with seven species represented. Bones of two or more species are frequently mixed together in pitfall deposits suggesting that all seven species were present throughout the 6000 to 1000 y BP time period. Different moa species could, however, have used the forest at different times of the year according to food availability.

The bones of *Anomalopteryx didiformis* are more than five times more frequent as those of the next most common species, *Dinornis struthoides* (Millener 1981a). This may not necessarily reflect their relative abundance as they are unlikely to have had similar foraging behaviour. If, for example, *A. didiformis* alone regularly included moist fern-covered hollows within its foraging range then its chances of falling into deep fissures or cave shafts would be increased.

The weights of species within this feeding guild ranged from 0.45 to c. 170 kg with large gaps in adult weights between some species (Table 6, Fig. 3). These gaps are to some extent more apparent than real because the weights of immature birds are

not included. Under natural conditions a more continuous distribution would have existed.

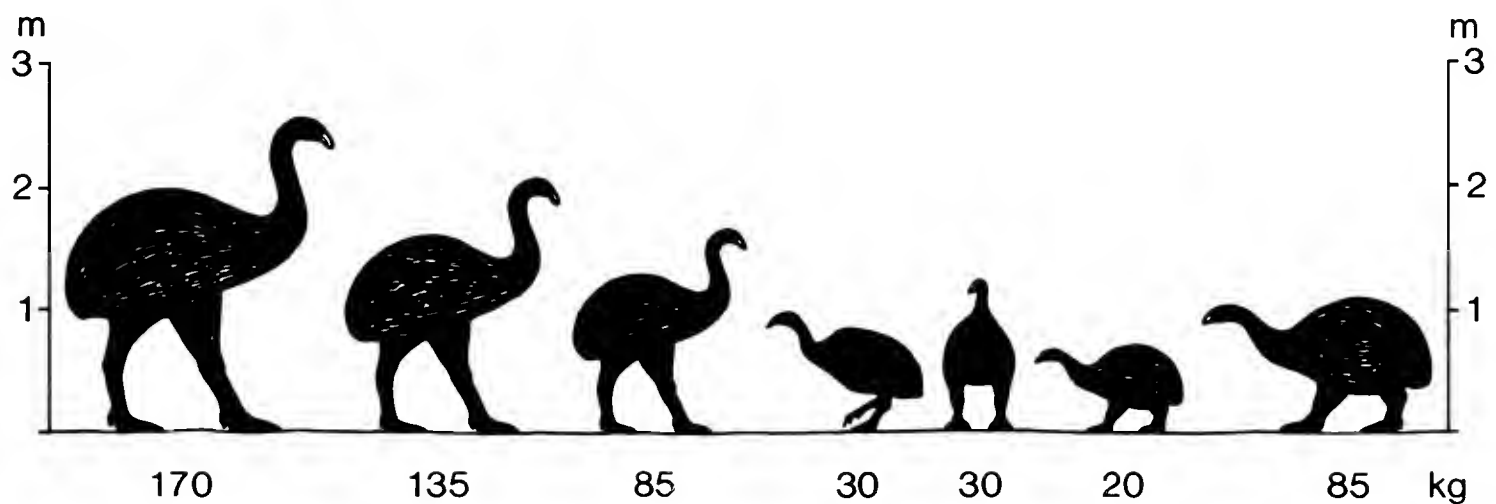


FIGURE 3 – Moas in the ground herbivore guild of the Waitomo region. From left to right: *Dinornis giganteus*, *D. novaezealandiae*, *D. struthoides*, *Anomalopteryx didiformis*, *Pachyornis mappini*, *Euryapteryx curtus*, *E. geranoides*. Estimated weights (kg) are shown for each species.

How did the members of this guild of comparatively large herbivores co-exist? Studies of mammalian herbivores in Africa have shown that the ability of these mammals to utilize food of poorer nutritional quality, i.e. foods high in structural carbohydrates such as cellulose, hemicellulose and lignin, is correlated with body size (Bell 1982). Larger body sizes are associated with adaptations for using low-quality herbage whereas smaller herbivores are more restricted to foods of high nutritional value. As a result, smaller herbivores generally tend to be more specialised in feeding behaviour (Owen Smith 1982).

The eight-fold difference in body weights between moa species of the Waitomo forest (Table 6) suggests that species differed substantially in the nutritional quality of the foods eaten. The three *Dinornis* species were broad-spectrum feeders, probably exploiting a variety of food plants daily, and were able to use herbage of poor nutritional quality (Burrows et al. 1981). This is consistent with the heavy weights (totaling up to 5 kg for *D. giganteus*) and large sizes of their gizzard stones (Gregg 1972, Burrows et al. 1981). Since both the ostrich and the rhea have hindgut modifications allowing significant fermentative digestion of fibre (McLelland 1979) it is probable that *Dinornis* spp., which apparently ate an even more fibrous diet, had similar specializations.

Although it has been suggested that *D. giganteus* was largely restricted to forest margins and other more open habitats (Anderson 1989, Worthy 1990), in the Waitomo region bones of at least 22 individuals of this largest moa occur in 8 (22%) of the caves examined (Millener 1981a). This indicates that it was a forest animal in this region. Its rarity is predictable from its great size and probable diet overlap with the other two species of *Dinornis* (Table 6) which had similar bill shapes and musculature. If the horizontal foraging patterns of these three species were broadly similar, the chances of any one species falling into a cave would vary according to its relative abundance; recoveries of bones of the three *Dinornis* species from caves in the Waitomo region have been in the approximate ratio of 3:2:1, the smallest species, *D. struthoides*, being the most frequent (Millener 1981a).

TABLE 6 – Foods and feeding behaviour of birds in the ground herbivore guild.

Ground herbivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Anomalopteryx didiformis</i> *	F. less/D	Foods unknown but (apparently specialised to utilize plants from soils of lower fertility as judged by base status and phosphorus levels; possibly larger component of animals in diet than other moas; browsing, gleaning and probing)	Lower understorey up to c. 1.3 m (Atkinson & Greenwood 1989)	c. 30	40	c. 30	-
<i>Pachyornis mappin</i> †	F. less/D	Foods unknown; (browsing)	Lower understorey up to c. 1.0 m (Atkinson & Greenwood 1989)	c. 30	-	c. 30	-
<i>P. elephantopus</i> *	F. less/D	Foods included <i>Phormium tenax</i> and the fern <i>Polystichum vestitum</i> (C.J. Burrows, pers comm) (Apparently adapted to eat leaves of very high fibre content, cf. Atkinson & Greenwood 1989); (browsing)	Lower understorey up to c. 1.8 m (Atkinson & Greenwood 1989)	-	145	-	-
<i>Emeus crassus</i> *	F. less/D	Foods included fruit, leaves or twigs of <i>Prumnopitys taxifolia</i> , <i>Coprosma rotundifolia</i> , <i>Pittosporum</i> sp. and thorns of <i>Rubus</i> sp. (Mason in Gregg 1972); (browsing).	Lower understorey up to c. 1.5 m	-	75	-	-
<i>Euryapteryx curtus</i> *	F. less/D	(Non-fibrous leaves and fruit; browsing)	Lower understorey up to c. 1.0 m (Atkinson & Greenwood 1989)	c. 20	-	c. 20	-
<i>E. geranoides</i> *	F. less/D	Foods included leaves and fruit of <i>Prumnopitys taxifolia</i> and fruit of <i>Muehlenbeckia australis</i> and <i>Rubus</i> sp. (Mason in Gregg 1972); (browsing)	Lower understorey up to c. 1.5 m (Atkinson & Greenwood 1989)	c. 85	95	c. 85	-
<i>Dinornis struthoides</i> *	F. less/D	Foods included parts of at least 16 forest or scrub species representing 13 families of angiosperms and gymnosperms. These foods included such high-fibre materials as twigs of <i>Dacrycarpus dacrydioides</i> and <i>Olearia virgata</i> , and leaves of <i>Podocarpus hallii</i> . Leaves of flax were also eaten (Burrows et al 1981 ³); (browsing)	Lower understorey up to c. 1.9 m (Atkinson & Greenwood 1989)	c. 85	95	c. 85	-

TABLE 6 – (Continued)

Ground herbivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>D. novaezealandiae</i> [*]	F. less/D	Foods unknown but (like other <i>Dinornis</i> spp, likely to have been a broad-spectrum feeder able to utilise high-fibre materials; browsing) [*]	Understorey up to c. 2.4 m (Atkinson & Greenwood 1989)	c. 135	145	c. 135	-
<i>D. giganteus</i> [*]	F. less/D	Foods included parts of at least 26 forest or scrub species representing 18 families of angiosperms and gymnosperms. These foods included such high-fibre materials as twigs or stems of various trees, shrubs and lianes, inner bark of <i>Plagianthus betulinus</i> , leaves of <i>Leptospermum scoparium</i> and <i>Pseudopanax ferox</i> (or <i>P. crassifolius</i>) and cladodes of <i>Phyllocladus alpinus</i> (Burrows et al 1981 ³); (browsing)	Understorey up to c. 2.9 m (Atkinson & Greenwood 1989)	c. 170	180	c. 170	-
<i>Porphyrio mantelli</i> Takahe	F. less/D	Leaf bases of tussock-forming grasses, sedges, rushes and composites, grass seeds, fern rhizomes; invertebrates fed to young chicks. Selective pulling of tillers or leaves followed by nipping and eating of basal parts. Foot used to hold tillers; raking with feet during early feeding of chicks (Gurr 1951, Mills & Mark 1977, Mills et al. 1980, 1984)	Ground and lower understorey	2.9; 2.5	2.9; 2.5	2.9; 2.5	-
<i>Gallinula hodgengi</i> [*] Hodgen's Rail	F. less/D	("shoots, stem bases of graminoids; invertebrates for chicks" Holdaway 1989a); (grazing and gleaning)	Ground and lower understorey	0.450	0.450	-	-
<i>Fulica chathamensis</i> [*] Chatham Island Coot	F. less/D	(shoots, leaves, seeds of terrestrial and aquatic plants, invertebrates; grazing and browsing)	Ground; aquatic in lagoons	-	-	-	c. 1.3

¹F = flighted; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.

²I = Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest

³The gizzard contents analysed by Burrows et al. 1981 from Scaifes Lagoon have since been identified as belonging to *Dinornis struthoides* (T.R. Worthy, pers. comm).

⁴As with *D. struthoides*, figures given for numbers of species eaten and plant families represented have been calculated on the assumption that gizzards of *D. giganteus* are restricted to the samples from Pyramid Valley.

^{*}Extinct species; brackets are used to indicate speculative inferences relating to such species.

How then were food resources partitioned between these three species? Atkinson and Greenwood (1989) gave measurements indicating that there was a differential of between 0.4 and 0.7 m between each pair of most similar-sized species in the heights they could stretch for food. Thus in times of food shortage, such as dry summers or cold winters, it could be expected that feeding by the most common species, *D. struthoides*, would deplete the understorey of foods suitable for *Dinornis* spp. Survival and thus coexistence of the two larger *Dinornis* spp. would then be possible only as a result of their height advantage.

The two species of *Euryapteryx*, judged by their U-shaped bills (Atkinson and Greenwood 1989), rather weak bill musculature (Cracraft 1980) and small stone sizes and total weights of gizzard stones (Worthy 1989), probably fed on plant parts low in fibre such as leaves, buds and fruit. Presumably the much smaller *E. curtus* was more specialised in feeding than *E. geranoides* although the height difference would have made some foods available only to the taller species.

The foods eaten by *Pachyornis mappini* are unknown although bill structure and cranial musculature (Cracraft 1980), suggest an animal adapted to cut fibrous leaves and stems. Fewer individuals are recorded from the Waitomo region (42) than of *E. curtus* (56) and *D. struthoides* (61), but *P. mappini* has been recovered from 12 (32%) of the caves studied (Millener 1981a).

The diet of *Anomalopteryx didiformis* is also unknown. Its formerly widespread distribution in a variety of forest habitats, including low fertility beech forests, suggests that it was specialized to feed on the most nutritious parts of the plants present. The studies of Emu by Davies (1978), Dawson and Herd (1983) and Herd and Dawson (1984) may provide a model for understanding *A. didiformis*. Weighing 28-48 kg, the Emu is comparable in size to this moa and is a generalized omnivore with high rates of passage and no large chambers in the gut for fermentative digestion. They forage widely for a wide range of high-quality foods such as insects, seeds, fruits, shoots and green herbage. Although emus avoid plant material high in lignins they can digest fibre rich in hemicellulose in the distal segment of the small intestine (Herd & Dawson 1984).

One of the more selective feeders among the ground herbivores present at Waitomo is likely to have been the Takahe *Porphyrio mantelli*. In their present alpine grassland habitat Takahe favour the basal meristems of tussock-forming grasses (Table 6), tissue low in fibre and rich in mineral nutrients, as well as fern rhizomes (Mills & Mark 1977). The gizzard is small (J.A. Mills, pers. comm.) and there are apparently no special hindgut modifications for microbial fermentation (Morton 1978). In lowland forest, suitable food plants such as the tussock grass *Cortaderia fulvida* occur along streambanks and a range of other plants including rhizomatous ferns grow within the forest itself. The recovery of Takahe bones from 14 (38%) of the caves studied, in association with bones of many obligate forest birds, suggests that Takahe were feeding in the forest even if not breeding there. Although Mills et al. (1984, 1988) identify Takahe as a relict species of Pleistocene grasslands, the evidence both from the Waitomo region and elsewhere points to Takahe as having been widespread in lowland forest although not necessarily very abundant (Millener & Templer 1981, Beauchamp & Worthy 1988, Caughley 1989).

The great depth of the Takahe's bill in relation to its width contrasts greatly with the proportions of a moa's bill and suggests that co-existence of Takahe with moas was achieved through differing modes of feeding as well as foods eaten.

TABLE 7 – Foods and feeding behaviour of birds in the arboreal herbivore, frugivore/herbivore and frugivore/insectivore guilds.

Arboreal herbivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habits			
				I	II	III	IV ²
<i>Cyanoramphus novaezelandiae</i> Red-crowned Parakeet	F/D	Buds, flowers, fruit, seeds, leaves, nectar, honeydew, invertebrates. Chatham Island : leaves, shoots, flowers, seeds. Browsing and gleaning (Taylor 1975, 1985)	Canopy, understorey, ground in forest and forest margins	0.085; 0.065	0.085; 0.065	0.085; 0.065	0.089; 0.074
<i>C. auriceps</i> Yellow-crowned Parakeet	F/D	Buds and shoots, flowers, seeds, leaves, many invertebrates including scale insects and caterpillars; browsing and gleaning (Taylor 1975, 1985)	Canopy, upper understorey, in closed forest	0.049; 0.039	0.049; 0.039	0.049; 0.039	- -
Frugivore/herbivores							
<i>Hemiphaga novaeseelandiae</i> N.Z. Pigeon	F/D	Fruit, leaves, flowers, ferns, seedlings; browsing, some grazing of herbs (McEwen 1978, Morris 1979)	Canopy, upper and lower understorey, ground	0.650	0.650	0.650	0.820
<i>Callaeas cinerea</i> Kokako	(F)/D	Fruit and leaves of a wide variety of species, particularly trees and shrubs, invertebrates including scale insects and bagmoths. Plucking/browsing and gleaning with food often held by foot (Hay 1981, Leathwick et al. 1983, Fitzgerald 1984, Powlesland 1987, Best & Bellingham 1990, pers. comm. from J. Innes, R. Hay and M. Clout)	Canopy and subcanopy; occ. use of understorey and ground	0.240	0.240	0.240	-
<i>Strigops habroptilus</i> Kakapo	F.less/N	Fruit, seeds, new shoots, leaves and petioles of a wide range of trees, shrubs, herbs, sedges and grasses; roots; rhizomes, rachis and petioles of mosses, club mosses and ferns. Browsing, grinding, husking and digging actions; grinding and chewing action of mandible and maxilla allows extraction of sap while fibrous tissue remains behind as compressed pellets, sometimes still attached to the plant. Foot used occasionally to hold food (Gray 1977, Best 1984, Merton 1985, Atkinson & Merton unpub.).	ground, sub-surface, lower and upper understorey	2.1; 1.3	2.1; 1.3	2.1; 1.3	-
Frugivore/insectivores							
<i>Nestor meridionalis</i> Kaka	F/D	Fruit, seeds, nectar, pollen, honeydew, sap exudate, scale insects and wood-boring invertebrates from both decaying and live wood. Plucking, husking, digging into wood, stripping and peeling bark, tapping and gauging holes into cambium, lapping nectar, pollen and sap. Foot often used to hold food (Beggs & Wilson 1987, O'Donnell & Dilks 1989a, Moorhouse 1991).	canopy, upper and lower understorey	0.505; 0.415	0.595; 0.500	0.505; 0.415	c.0.500; c.0.400

¹ F = flightless; F.less = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.

² I = Waitomo conifer/hardwood forest; II = Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.

The smallest member of the ground herbivore guild at Waitomo was *Gallinula hodgeni* which is only present rarely in bone deposits, and which probably fed mostly in riparian vegetation within or adjacent to the forest. The New Zealand Coot *Fulica prisca* although present at Waitomo, is principally a water-bird and has, therefore, not been included in the ground herbivore guild.

Arboreal herbivores, frugivore/herbivores and frugivore/nectivores (Table 7, Figure 4)

Strict arboreal herbivores are limited to two species of parakeet both of which eat principally buds, flowers and seeds. However the smaller Yellow-crowned parakeet *Cyanoramphus auriceps* includes a significant proportion of insects in its diet, particularly during the breeding season (R.H. Taylor, pers. comm.) and the Red-crowned Parakeet *C. novaezealandiae* forages on the ground and in forest openings or margins.

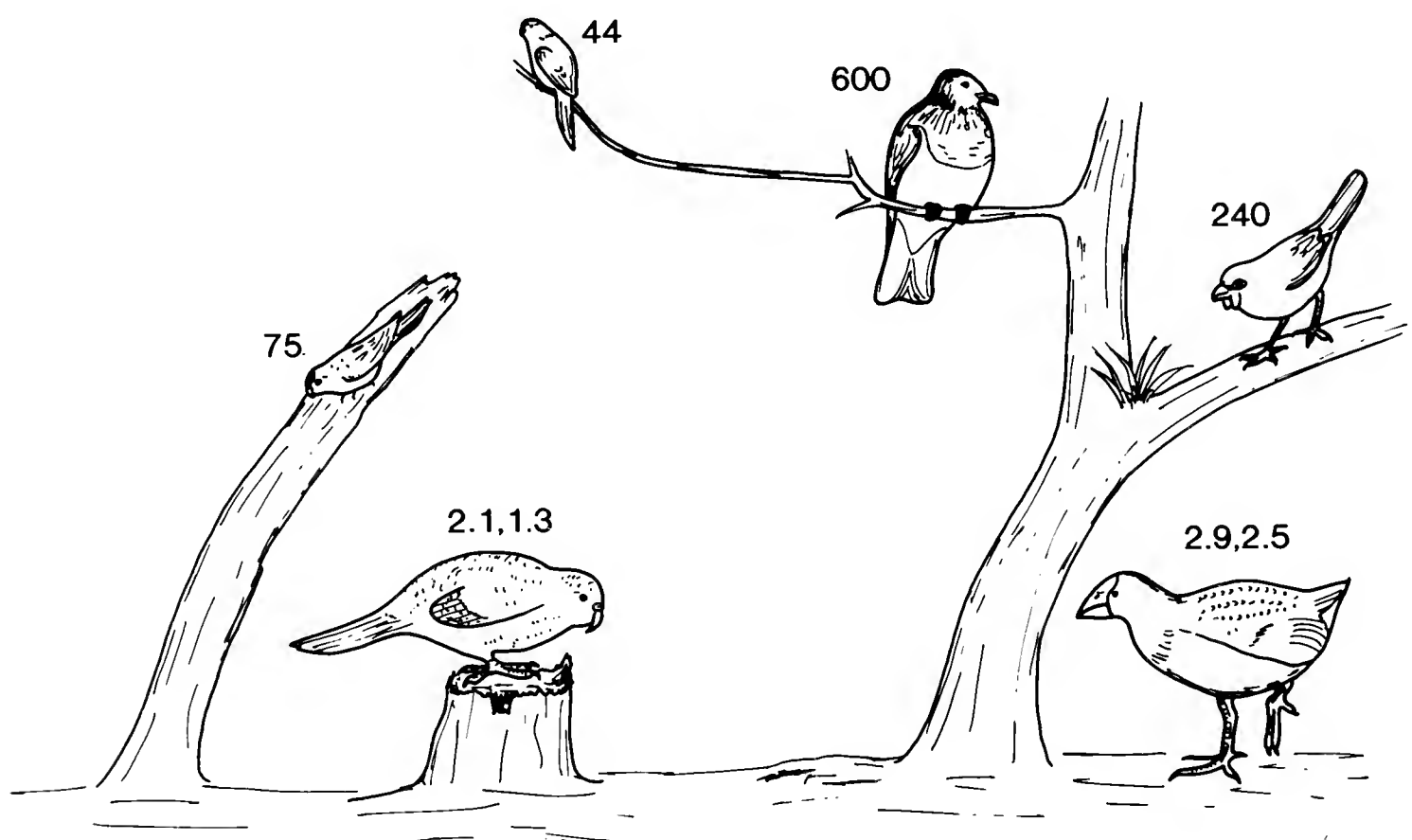


FIGURE 4 – Arboreal herbivores and frugivore/herbivores in the Waitomo region. From left to right: Red-crowned Parakeet, Kakapo, Yellow-crowned Parakeet, N.Z. Pigeon, Kokako. Figures show weights in g except Kakapo (kg); male weights precede female weights (see Table 7).

The Pigeon *Hemiphaga novaeseelandiae*, Kokako *Callaeas cinerea* and Kakapo *Strigops habroptilus*, although mainly leaf-eating, are here classified as frugivore/herbivores, because their successful breeding appears dependent on adequate supplies of fleshy fruit. Kokako may sometimes breed earlier than Pigeons, thus allowing the two species to use fruit that ripen at different times, but there is overlap in their breeding seasons. Pigeons do not take insects but the significance of small insects fed by Kokako to nestlings as a further mechanism for ecological separation of the two species is unknown.

The reduced flight powers of Kokako may have made them more vulnerable than Pigeons to entrapment in caves but Millener (1981a) recorded nearly four times as many Kokako as Pigeons in the Waitomo cave deposits.

TABLE 8 – Foods and feeding behaviour of birds in the nectivore guild.

Nectivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Notiomystis cincta</i> Stitchbird	F/D	Nectar, fruit invertebrates; the most frugivorous of the three honeyeaters; lapping, plucking and gleaning (Gravatt 1971, Gaze & Fitzgerald 1982, Angehr 1986)	Upper and lower understorey, canopy	0.038; 0.030	- -	0.038; 0.030	- -
<i>Anthornis melanura</i> Bellbird	F/D	♂ : Nectar, honeydew, invertebrates, fruit; ♀ : invertebrates, nectar, honeydew, fruit; the most insectivorous of the three honeyeaters; lapping, gleaning from trunks and branches, plucking (Gravatt 1971, Norton, 1980, Gaze & Fitzgerald 1982, Gaze & Clout 1983, Angehr 1986)	Upper and lower understorey, canopy	0.031; 0.024	0.031; 0.024	0.031; 0.024	c.0.035
<i>Prosthemadera novaeseelandiae</i> Tui	F/D	Nectar and honeydew, fruit invertebrates; the most nectivorous of the three honeyeaters; lapping, plucking and gleaning (Gravatt 1971, Gaze & Fitzgerald 1982, Gaze & Clout 1983, Angehr 1986)	Canopy, subcanopy, upper understorey	0.125; 0.090	0.125; 0.090	0.125; 0.090	c.0.125; c.0.090

¹ F = flighted; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.
² Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.

The flightless nocturnal Kakapo is not only the world's heaviest parrot but the only lek breeding member of the Psittacidae (Merton et al. 1984). Its feeding habits are unique. The tip of the mandible rolls and crushes plant material against a series of serrated transverse ridges and grooves on the ventral surface of the maxilla. This allows sap and other juices to be extracted from leaves that are eaten while the fibre is rejected as pellets (Gray 1977, Merton 1985). The gizzard is relatively small and the extrusion of fibre during feeding means that no hindgut modifications are required for fibre digestion. Kakapo climb readily and feed arboreally as well as on the ground with other ground herbivores. Like the Takahe they feed very selectively but, unlike the gallinule, Kakapo eat an extremely wide range of species (Table 9). Kakapo breed later than Pigeons and Kokako and their apparent dependence on fruit (or possibly grass seed) during the nestling period in late summer, rather than insects, suggests that they did not compete with these species for food during the breeding season. Judged by the numbers of individuals recovered, Kakapo together with *Anomalopteryx didiformis* were the two most common flightless herbivores in the Waitomo forest.

Fruit are also a crucial component of the diet of Kaka *Nestor meridionalis* but this parrot eats a large variety of high-protein foods not used by Pigeon, Kokako or other parrots in lowland forest (Table 7).

Nectivores (Table 8)

The New Zealand avifauna has no birds dependent mainly on nectar for much of the year, unlike that of Australia where nectar is more generally available. Nevertheless, because the three species listed in Table 8 are all Meliphagid honeyeaters with well developed brush tongues (McCann 1964) and all use nectar as a major food source, it is convenient to group them as a nectivore guild.

The largest of the three species, the Tui *Prosthemadera novaeseelandiae* is the most dependent on nectar (Gravatt 1971). It is also the most aggressive, driving other honeyeaters and other birds away from trees where it feeds. A social hierarchy has been demonstrated by Craig (1984, 1985) in which Tuis dominate over Bellbirds *Anthornis melanura* which in turn dominate Stitchbirds *Notiomystis cincta*. Intraspecific dominance also occurs.

The three species differ in their use of certain flowers as well as in the seasonal proportions of fruit and insects taken, especially in winter (Gravatt 1970, 1971, Table 8). Bellbirds are more insectivorous during autumn and winter while Tuis and Stitchbirds rely more on fruit at this time. Kaka when feeding on nectar or honeydew, also become part of the nectivore guild (Table 7).

Aquatic insectivores (Table 9)

This guild of three ducks was closely related to the riparian system within the forest and its associated habitats. Blue duck *Hymenolaimus malacorhynchos* are specialized to feed in turbulent or fast-flowing water and probably made little use of the forest itself beyond the stream banks. Finsch's Duck *Euryanas finschi* may have foraged extensively on land as suggested by Worthy & Mildenhall (1989) but the particular use it made of its very short bill is unknown. This species is the commonest guild member at Waitomo, perhaps because it may have nested in caves (McCulloch 1975). Brown Teal *Anas aucklandica* can use vegetated areas beyond stream courses where its nocturnal feeding may have allowed it to take foods unavailable to other members of the guild.

TABLE 9 – Foods and feeding behaviour of birds in the aquatic insectivore guild.

Aquatic Insectivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Anas aucklandica</i> Brown Teal	F/N,D	Insects, worms, snails, succulent shoots and roots; nocturnal foraging in heavily vegetated wetlands, diurnal dabbling and diving in still or slow-flowing water (McKenzie 1971, Weller 1974, Williams 1985a)	aquatic, ground	0.600; 0.540	0.600; 0.540	0.600; 0.540	0.600; 0.540
<i>Hymenolaimus malacothynchos</i> Blue Duck	F/D	Aquatic invertebrates, particularly case-living and free-living caddis larvae. Underwater searching of rocks with head and neck submerged, upending or diving in deeper water, both activities concentrated in turbulent or fast-flowing water, occasional sieving of water from bank (Kear & Burton 1971, Williams 1985b, Harding 1990).	aquatic; ground	0.900; 0.765	-	-	-
<i>Euryanas finschi</i> Finsch's Duck	(F)?D	("Invertebrates, fallen fruit"); (terrestrial foraging in wet vegetation, dabbling in streams) (Holdaway 1989, Worthy & Mildenhall 1989)	aquatic; ground	c.2.25	c.2.25	c.2.25	-

¹ F = flightless; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.

² Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.

• Extinct species; brackets are used to indicate speculative inferences relating to such species.

TABLE 10 – Foods and feeding behaviour of birds in the ground insectivore guild.

Ground Insectivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Apteryx owenii</i> Little Spotted Kiwi	F.less/N	Earthworms, crane-fly larvae and pupae, grass grub beetle larvae, caterpillars, spiders, and fruit of hinau, toro and pigeonwood (Peat 1990). Probing of soil and gleaning of leaf litter	Ground; subsurface to depths of 70 mm (♂) and 80 mm (♀)	1.2; 1.3	-	1.2; 1.3	-
<i>A. australis</i> Brown Kiwi	F.less/N	Invertebrates, particularly earthworms and cicada larvae, fruit, seeds, freshwater crayfish (Reid et al. 1982). Probing of soil and gleaning of leaf litter	Ground; subsurface to depths of 100 mm (♂) and 130 mm (♀)	2.1; 2.5	?	2.1; 2.5	-
<i>Diaphorapteryx hawkinsi</i> * giant Chatham I. Rail	F.less/?	(Invertebrates, fallen fruit leaves, ? petrel chicks). Gleaning of litter and probing of soil	Ground; subsurface	-	-	-	c.2.0
<i>Rallus dieffenbachii</i> ^{3*} Dieffenbach's Rail	F/D	(Invertebrates, fruits, seeds). Gleaning of litter and probing of soil	Ground; subsurface	-	-	-	c.0.370
<i>R.modestus</i> * Chatham I. Rail	F.less/N	(Invertebrate, fruits, seeds). Gleaning and probing (Travers & Travers 1873).	Ground	-	-	-	c.0.060
<i>Capellirallus karamu</i> * N.Z. Snipe-rail	F.less/?	(Invertebrates. Gleaning of litter and deep probing in soft soil) (Holdaway 1989a).	Ground; subsurface	c.0.275	-	c.0.275	-
<i>Gallirallus australis</i> Weka	F.less/D,N	Invertebrates, particularly beetles and wetas, snails, lizards, fallen fruit, leaves, seeds; gleaning and raking of litter with bill; shallow probing after rain (Carroll 1963, Coleman et al. 1983, Robertson & Beauchamp 1985, pers. comms from A.J. Beauchamp and H.A. Robertson)	ground, subsurface, aquatic	0.950; 0.700	0.910; 0.690	0.950; 0.700	-

TABLE 10 – (Continued)

Ground Insectivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Coenocorypha aucklandica</i> N.Z. Snipe	F/N,D	Invertebrates of litter, sedges and tussock bases amongst dense ground cover. Gleaning and probing of humus, soil and vegetation. (Fleming 1939, Anderson 1968, authors' observations)	Ground; subsurface	0.088	0.088	-	-
<i>C. chathamica</i> * extinct Chatham Island Snipe	F/N,D?	(Invertebrates of litter amongst dense ground cover. Gleaning and probing of humus, soil and vegetation)	Ground; subsurface	-	-	-	c.0.105
<i>Traversia lyallii</i> * Stephens I. Wren	F.less/N	Invertebrates on surface of litter and logs obtained by semi-nocturnal gleaning (Buller 1896).	ground	0.022	-	-	-
<i>Pachyplichas jagmi</i> * North I. Stout-legged Wren	(F)/D?	Invertebrates (obtained from thick undergrowth and decaying logs by gleaning and probing)	(ground and ground storey)	0.040	-	-	-
<i>P.yaldwyni</i> * South I. Stout-legged Wren	(F)/D?	Invertebrates (obtained from thick undergrowth and decaying logs by gleaning and probing)	(ground and ground storey)	-	0.050	-	-
<i>Petroica australis</i> N.Z. Robin	F/D	Invertebrates including earthworms, spiders, wetas, stick insects, cicadas, snails, slugs, moths, caterpillars, beetles; berries taken occasionally in summer and autumn. Pouncing, gleaning and raking with bill, often accompanied by flushing with wing tips or vibrating of foot (Powlesland 1981, Flack 1985)	ground, ground storey, lower understorey	0.037; 0.035	0.037; 0.035	0.037; 0.035	- -
<i>P. traversi</i> Black Robin	F/D	Broad range of invertebrates, particularly wetas, larvae and scale insects. Pouncing on and gleaning from ground and bark surfaces, raking with bill, sometimes accompanied by vibrating of foot (Flack & Merton 1985, D.V. Merton, pers comm.)	ground, ground storey, lower understorey	- -	- -	- -	0.024; 0.021

¹ F = flighted; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.

² I = Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.

³ Dieffenbach's rail is so much larger than *R.phillipensis* that specific status, as adopted by G.R. Gray in Dieffenbach (1843), is justified.

* Extinct species; brackets are used to indicate speculative inferences relating to each species.

Ground insectivores (Table 10, Figure 5)

The largest guild members are the kiwis, nocturnal ratites specialized for probing for earthworms, particularly those of the subsoil. The extinct flightless Snipe-rail *Capellirallus karamu*, possibly a diurnal forager, is likely to have used its exceptionally long and slender bill for taking subsurface invertebrates also. The smallest member of this subsurface-feeding group, the insectivorous New Zealand Snipe *Coenocorypha aucklandica*, was formerly widespread on the mainland but is now restricted to outlying islands.

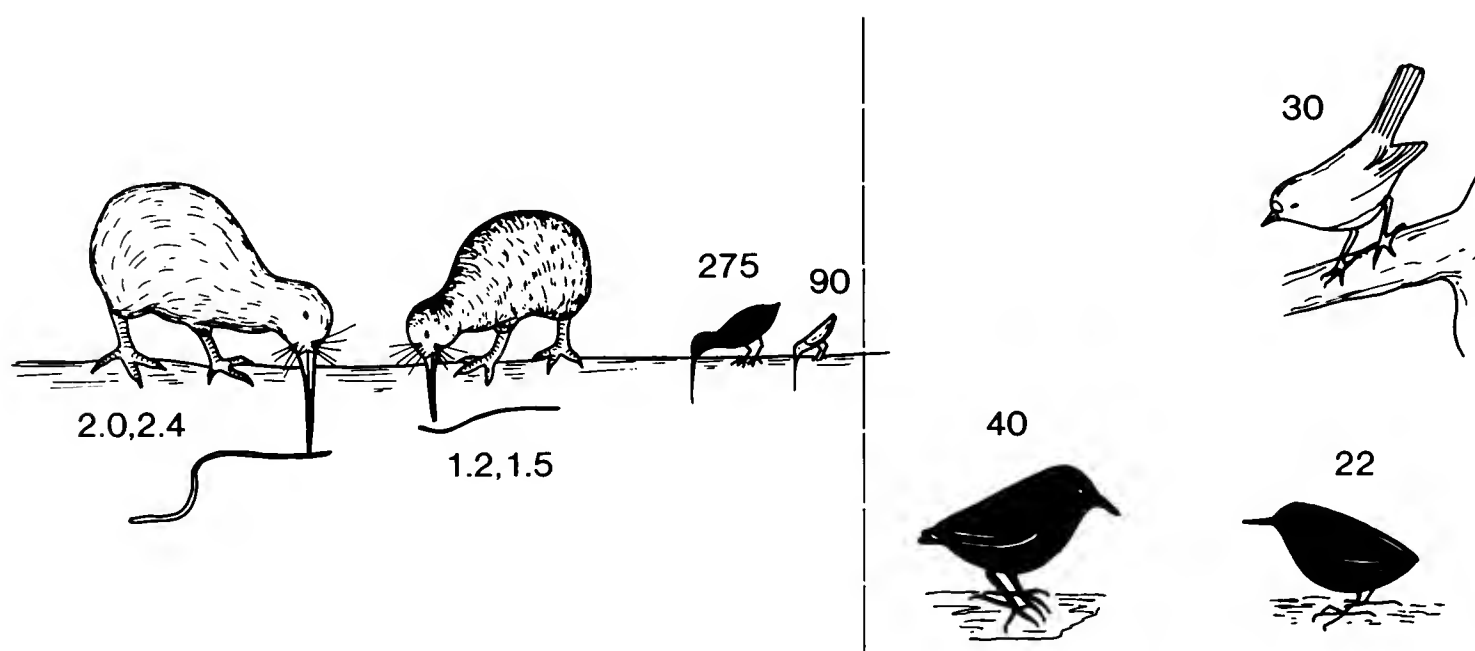


FIGURE 5 – The ground insectivore guild in the Waitomo region. From left to right: Brown Kiwi, Little Spotted Kiwi, Snipe-rail, N.Z. Snipe, North Island Stout-legged Wren, Travers' Wren and Robin (top right). Figures show weights in g except kiwis (kg); male weights precede female weights. Extinct species silhouetted. Three passerines at right drawn to larger scale than sub-surface feeders at left. Not shown is the Weka (see Table 10).

Between them, these four species could probe depths to 130 mm in a series of overlapping ranges - Snipe to c. 45 mm, Snipe-rail to c. 56 mm, Little Spotted Kiwi *Apteryx owenii* to c. 80 mm, and Brown Kiwi *A. australis* to c. 130 mm. As bill length differs markedly between sexes in the kiwis (Colbourne & Kleinpaste 1983) subsurface foods may have been partitioned even more than indicated by these figures. None of the living species in this group restrict their feeding to subsurface levels and it is unlikely that the Snipe-rail did so either.

The most important ground-surface insectivore is likely to have been the Weka *Gallirallus australis* which is common in the Waitomo deposits and which forages continually through litter but only rarely probes and then shallowly (Table 10). Three small passerines were also ground-surface foragers in the Waitomo region (Figure 5). The North Island Stout-legged Wren *Pachyplichas jagmi* had at best only weak powers of flight and may have used its relatively powerful legs to thrust its way into thicker undergrowth or decaying logs to find invertebrates unavailable to other small members of the guild. The Stephens Island Wren *Traversia lyalli* is the world's smallest flightless passerine (Millener 1989). It apparently foraged mostly at dusk, a time when amphipods in the litter become very active (M.J. Meads, pers. comm.).

The third passerine insectivore in this guild was the Robin *Petroica australis* whose method of feeding is to survey an area of ground from a perch and then pounce from

above. Robins forage whenever litter is disturbed. If any of the moas habitually used their huge feet to rake over litter in searching for small animals, fruit, or fern rhizomes, many diurnal insectivores in this guild would have benefitted from the disturbance to their prey.

Smaller arboreal insectivores: < 50 g wt (Table 11, Figure 6)

The arboreal insectivore guild is separated here into two groups based on size. This is an arbitrary distinction for convenience although large size differences are correlated with differences in modal prey size.

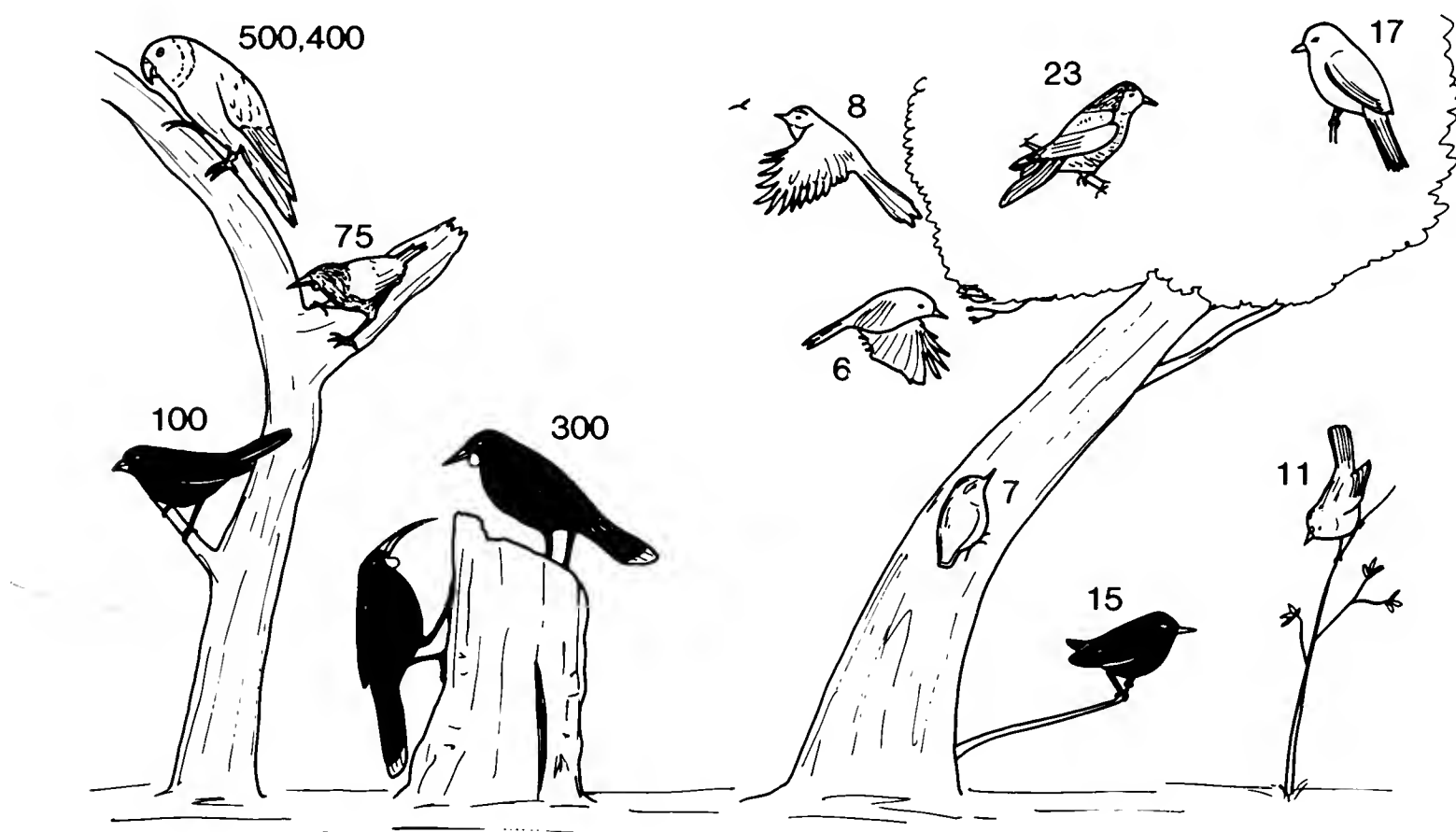


FIGURE 6 – The arboreal insectivore guild in the Waitomo region with the only frugivore/insectivore, the Kaka, at top left. Other birds from left to right: Piopio, Saddleback, Huia (male, female), Fantail, Grey Warbler, Rifleman, Shining Cuckoo, Bush Wren, Tomtit and Whitehead (top right). All weights in g. Extinct species silhouetted. Smaller insectivores at right drawn at larger scale than larger insectivores at left. The nocturnal and semi-nocturnal members of this guild are not shown (see Tables 11, 12).

Each of the seven small birds in this group appears to be separated by different combinations of feeding level, feeding station, mode of feeding and sometimes kind of prey taken. The heaviest member of the group, the Shining Cuckoo *Chrysococcyx lucidus* is a summer migrant taking invertebrates that are largely unpalatable to other birds; the Rifleman *Acanthisitta chloris* gleans and probes on trunks and branches; the Whitehead *Mohoua albicilla* takes insects and fruit from foliage and twigs within the crowns of trees in the upper understorey and canopy; the Grey Warbler *Gerygone igata* feeds through the full height range of the forest but hovers in order to take prey from the tips of terminal shoots and leaves; and the Fantail *Rhipidura fuliginosa* is specialized for hawking insects on the wing.

The two remaining birds in this group, the Bush wren *Xenicus longipes* and the New Zealand tomtit *Petroica macrocephala* concentrate their feeding between lower understorey and the ground. Information is insufficient but in common with many other co-existing insectivores they probably foraged in different kinds of places.

TABLE 11 – Foods and feeding behaviour of birds in the arboreal insectivore guild. (a) smaller arboreal insectivores (< 50 g body weight).

Smaller arboreal Insectivores	Fllgh/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Chrysococcyx lucidus</i> Shining Cuckoo	F/D	Insects, mainly caterpillars and beetles unpalatable to other birds; gleaning of foliage, sometimes with vigorous shaking (Grimmett 1922, Smith 1923, Blackburn 1963, Gill 1980a)	canopy, upper understorey	0.023	0.023	0.023	0.023
<i>Acanthisitta chloris</i> Rifleman	F/D	Beetles, spiders, weevils, moths, caterpillars; gleaning, probing and prising on trunks and branches (Gravatt 1971, Gray 1974, Moeed & Fitzgerald 1982, Fitzgerald et al. 1989)	Upper understorey	0.006; 0.008	- -	- -	- -
<i>Xenicus longipes</i> Bush Wren	F/D	Invertebrates; gleaning of foliage, trunks, branches, lichens, mosses and litter, especially the latter disturbed by other birds. Feeding accompanied by bobbing action (Potts 1873, Falla et al. 1987)	understorey, ground storey, ground	0.015	-	0.015	-
<i>Bowdleria punctatus</i> Fernbird	(F)/D	Invertebrates, including spiders, caterpillars and hemipterans, gleaned from open shrubland or forest margins (Best 1979, Barlow & Moeed 1980)	ground, ground storey, lower understorey	- -	- -	0.036; 0.034	- -
<i>B. rufescens</i> * Chatham I. Fernbird	(F)/D	Invertebrates gleaned from shrublands, rushlands and forest (Travers & Travers 1873)	ground, ground storey, lower understorey	-	-	-	c.0.039
<i>Mohoua novaeseelandiae</i> Brown Creeper	F/D	Invertebrates gleaned or probed from trunks, under bark, foliage, branches and twigs, some fruit (Gill 1980b, J.B. Cunningham 1984, 1985)	upper understorey including subcanopy, occasionally lower understorey	- -	0.013; 0.011	- -	- -
<i>M. albicilla</i> Whitehead	F/D	Beetles, caterpillars, spiders, fruit by gleaning of leaves and twigs. Feet used frequently to hold food items (Gibb 1961, Gravatt 1971, Moeed & Fitzgerald 1982)	canopy, upper understorey	0.019; 0.015	- -	0.019; 0.015	- -
<i>Gerygone igata</i> Grey Warbler	F/D	Beetles, moths, caterpillars, spiders taken from leaves and terminal shoots by gleaning, hovering and hawking (Gibb 1961, Gravatt 1971, Moeed & Fitzgerald 1982, Gill 1983)	Upper and lower understorey, canopy	0.006	0.006	0.006	-

TABLE 11 – (Continued)

Smaller arboreal Insectivores	Flight/Activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>G. albofrontata</i> Chatham I. Warbler	F/D	Invertebrates including flies, beetles, caterpillars, moths, cicadas, bugs and spiders; gleaning on trunks and branches as well as from leaves and crevices, some hovering (Robertson 1985, D.V. Merton, pers. comm)	understorey, ground	-	-	-	0.011 0.010
<i>Rhipidura fuliginosa</i> Fantail	F/D	Beetles, moths, flies, wasps taken by hawking; prey flushed from vegetation by fanning of tail and momentary wing spreading as well as by disturbance during feeding with other birds. Feet used to clamp larger food items during dismemberment. (Gibb 1961, Moeed & Fitzgerald 1982, Fitzgerald et al. 1989, McLean 1989, authors' observations)	above canopy, canopy, understorey, ground storey	0.008	0.008	0.008	0.008
<i>Petroica macrocephala</i> N.Z. Tomtit	F/D	Beetles, weevils, flies, moths, caterpillars, wetas, bugs, spiders, millipedes and earthworms taken by snatching, pouncing, gleaning, hovering and hawking (Gibb 1961, Gravatt 1971, Moeed & Fitzgerald 1982, Fleming 1985, Fitzgerald et al. 1989).	lower understorey, ground storey and ground	0.011	0.011	-	0.016

¹ F = flighted; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.
² I = Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.
• Extinct species.

TABLE 12 – Foods and feeding behaviour of birds in the arboreal insectivore guild. (b) larger arboreal insectivores (> 50 g body weight).

Larger arboreal insectivores	Flight/activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Cyanoramphus forbesi</i> Forbes' Parakeet ³	F/D	Invertebrates, mainly caterpillars and scale insects, flowers, seeds; gleaning (Taylor 1975, 1985)	canopy, ground	-	-	-	0.086 0.065
<i>Eudynamys taiteensis</i> Long- tailed Cuckoo	F/D, N	Invertebrates, including beetles, wetas and stick insects; lizards, small birds and their eggs, seeds; gleaning and pouncing (Oliver 1955, Gill 1980c, Reed 1980, J.M. Cunningham 1985)	Canopy, understorey, ground	0.125	-	0.125	-
<i>Ninox novaeseelandiae</i> Morepork	F/N	Invertebrates, especially moths and moth larvae, beetles, wetas and spiders; lizards, birds and their young, bats. Hawking and pouncing (Lindsay & Ordish 1964, Saint Girons et al. 1986, Falla et al. 1987).	above canopy, canopy understorey, ground	0.175	0.175	0.175	-
<i>Sceloglaux* albifacies</i> Laughing owl	F/N	Invertebrates, particularly earthworms and insects; lizards, small birds, ? bats (Williams & Harrison 1972, Falla et al. 1987) (Pouncing)	forest edge, open ground	c.0.500	c.0.500	c.0.500	-
<i>Megaegotheles* novaeseelandiae</i> N.Z. Owllet-nightjar	(F)/N	(*Large invertebrates, frogs, lizards* Holdaway 1989) (Pouncing)	(understorey, ground)	c.0.200	c.0.200	c.0.200	-
<i>Halcyon sancta</i> N.Z. Kingfisher	F/D	Large invertebrates, particularly cicadas, dragonflies, beetles and chafer; blowflies; lizards, small birds, crabs more especially in winter. Modal size of prey for insects : 20-30 mm. Pouncing, (Lewis 1959, O'Donnell 1981, Fitzgerald et al. 1986, Hayes 1989)	canopy, understorey, ground, aquatic, intertidal	-	-	0.065	-
<i>Philesturnus carunculatus</i> Saddleback	F/D	Invertebrates, particularly caterpillars, beetle larvae, spiders, centipedes and wetas; fruit. Probing, prising, stripping and gleaning; foot used occasionally to hold food item (Atkinson 1964, 1966b, Merton 1966)	canopy, upper and lower understorey, ground	0.081; 0.069	0.085; 0.072	0.081; 0.069	- -

TABLE 12 – (Continued)

Larger arboreal Insectivores	Flight/activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Heteralocha acutirostris</i> * Huia	(F)/D	Larger invertebrates, particularly larvae of wood-boring beetles, adult beetles, caterpillars, wetas, spiders; fruit. Food taken by probing and chiselling with bill, under bark and into decaying wood (♂) or into larval chambers in harder wood (♀). (Falla et al. 1987)	Understorey, ground storey, ground	0.295	-	0.295	-
<i>Tumagra capensis</i> * Piopio	F/D	Invertebrates, fruit, seeds, foliage. Gleaning and sometimes turning of litter, occasional hawking (Potts 1873).	Ground, ground storey, understorey, canopy	c.0.100	c.0.100	c.0.100	-

¹ F = flighted; F.less = flightless; (F) = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.
² I = Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.
³ Genetic studies by Triggs and Daugherty (in press) show that Forbes' Parakeet deserves specific status as recognised by Rothschild (1893).
* Extinct species; brackets are used to indicate speculative inferences relating to such species.

Larger arboreal insectivores: > 50 g wt (Table 12, Figure 6)

This part of the insectivore guild contains both generalists and specialists. The largest of the generalists is the Long-tailed Cuckoo *Eudynamys taitensis*, a summer migrant that eats a wide range of small animals from all levels in the forest and which possibly also feeds at night. The extinct Piopio *Turnagra capensis* included invertebrates as an important part of its diet but also ate fruit, seeds and foliage, and could perhaps be classified as an omnivore.

Both the Saddleback *Philesturnus carunculatus* and the extinct Huia *Heteralocha acutirostris* are specialized to take invertebrates by probing into living or dead wood. The much greater size and strength of the Huia, together with its marked sexual dimorphism in bill shape, allowed the Huia to extract invertebrates from a wider range of woody substrates too difficult for Saddlebacks to use.

Three nocturnal insectivores are also included in this guild; two raptors and an Owlet-nightjar. The largest of the raptors, the extinct Laughing Owl *Sceloglaux albifacies* probably foraged in forest openings and along forest edges and is only rarely present in the Waitomo cave deposits. The much smaller Morepork *Ninox novaeseelandiae*, which hunts both in forest and forest edges, is equally rare in these deposits. The extinct Owlet-nightjar *Megaegotheles novaezealandiae* is much better represented in the Waitomo region than either of the nocturnal raptors. Its diet is unknown but large flightless insects and nocturnal moths would have been potential foods.

When feeding on wood-boring insects the Kaka parrot would be functioning as a member of this guild as would Kokako when taking foliage insects (Table 7). It should not be forgotten that some members of this guild could at times be in competition with bats for food.

Major predators of vertebrates (Table 13)

At Waitomo this guild consisted of four species, three of them diurnal raptors. The largest of the raptors was the extinct *Circus eylesi* whose phylogenetic relationship is with the harriers *Circus* spp. but whose morphology, particularly wing shape, suggests that it behaved more like a goshawk (Holdaway 1989, pers. comm). It probably preyed on medium-sized birds by rapid pursuit through the forest from a perch rather than hovering or soaring to find prey. Thus moa chicks are likely to have been part of its diet. The much smaller falcon *Falco novaeseelandiae* is little more than a tenth of the weight of *C. eylesi* and takes much smaller prey from both perching and soaring positions. The harrier *C. approximans* specializes in stationary or slow-moving prey and carrion. Food is sighted while soaring, possibly assisted by hearing for live prey.

The feeding habits of the North Island Aptornis *Aptornis otidiformis* are something of an enigma. The position of the eye orbits suggests it had binocular vision. R.L. Zusi (pers. comm.) has found evidence of very heavy musculature in the upper neck region behind the skull which he considers gave the bird considerable levering or wedging power. The bill is large and broad, angled at the edges and both flattened and slightly downcurved at the tip. Gizzard stones have not been recorded with bones of Aptornis. Thus this bird may have fed by tearing open rotten logs or digging for invertebrates, Tuatara, or petrels in shallow burrows (Holdaway 1989).

TABLE 13 – Foods and feeding behaviour of birds in the guild of major predators of vertebrates.

Major predators of vertebrates	Flight/activity ¹	Foods/methods of feeding	Feeding level	Representative body wts (kg) in reconstructed habitats			
				I	II	III	IV ²
<i>Falco novaeseelandiae</i> N.Z. Falcon	F/D	Passerine birds and nestlings, insects on wing, lizards taken by pouncing, snatching or hawking from perch or soaring position (Oliver 1955, Fitzgerald 1965, Fox 1985).	above canopy, canopy, understorey, ground	0.265; 0.460	0.265; 0.460	0.265; 0.460	c.0.265; c. 0.460
<i>Circus approximans</i> Australasian Harrier	F/D	Passerine birds, eggs and nestlings, carrion, ducks, lizards, insects including crickets, grasshoppers and cicadas taken from soaring position (Carroll 1968, Redhead 1968, 1969, Baker-Gabb 1981)	canopy, subcanopy, ground	0.650; 0.840	0.650; 0.840	0.650; 0.840	0.650; 0.840
<i>C.eylesi</i> *	F/D	("Kaka, Kakapo, Pigeon, Finsch's Duck, Weka, Kokako" Food taken by snatching or pouncing following rapid pursuit from perch. Holdaway 1989, pers comm.).	(above canopy, canopy, understorey, ground)	c.2.5 c.3.0	c.2.5 c.3.0	c.2.5 c.3.0	- -
<i>Harpagornis moorei</i> * extinct NZ Eagle	F/D	("Large to very large ground birds of up to 250 kg" e.g. geese, <i>Aptornis</i> , moas. Pouncing. "Prey taken by powerful strike after rapid descent from high perch" Holdaway 1989)	ground	- -	c.9.5 c.12.5	- -	- -
<i>Haliaeetus australis</i> * extinct Chatham I. Sea Eagle	F/D	(Waterbirds and their chicks, rails, seabirds, fish, carrion. Striking and snatching, robbing prey from other birds)	above canopy, ground, aquatic, marine	-	-	-	+
<i>Aptornis otidiformis</i> * North I. Aptornis	F.less/D	("Large invertebrates, frogs, lizards, tuatara, petrels and petrel chicks" Holdaway 1989. ? Land slugs. Gleaning, prising and digging)	ground, ground storey, subsurface	c.10- 11.0	-	c.10- 11.0	-
<i>Aptornis defossor</i> * South I. Aptornis	F.less/D	("Large invertebrates, frogs, lizards, tuatara, petrels and petrel chicks" Holdaway 1989. ?Land slugs. Gleaning, prising and digging)	ground, ground storey, subsurface	-	c.12- 13.0	-	-
<i>Catharacta skua</i> Brown Skua	F/N,D,	Broad-billed prions, White-faced Storm Petrels, other small petrels. Running beneath forest canopy and snatching (Young et al. 1988)	ground	- -	- -	- -	1.7; 1.8
Carrion feeders							
<i>Palaeocorax moriorum</i> * extinct N.Z. Crow	(F)/D	(Carrion from moas, petrels, fish, seals, etc, large insects, lizards, fruit. Gleaning, snatching, pouncing : opportunistic feeder. Holdaway 1989).	ground, understorey and canopy, often near coast	0.950	0.950	0.950	0.950

¹ F = flightless; F.less = weak or reduced flight powers; D = diurnal; N = nocturnal; N,D = both activities observed.
² I = Waitomo conifer/hardwood forest; II = N. Canterbury conifer/hardwood forest; III = Northern Capes coastal forest; IV = Chatham I. coastal forest.
* Extinct species; brackets are used to indicate speculative inferences relating to such species.

II. COOL-TEMPERATE DRY CONIFER/HARDWOOD FOREST ON LOESS-COVERED HILLS AND VALLEYS

Site description

This reconstruction takes in an area of low hills with limestone outcrops and valleys in North Canterbury between 100 and 400 m altitude (Figure 7). Mean annual temperature varies between 10 and 12.5°C and annual rainfall is between 750 and 1000 mm. The Pyramid Valley swamp is central to this reconstruction but data from other swamps and a few caves within 20 km of this swamp are included. Miocene limestones form the basement rock at Pyramid Valley (Gregg 1972) but alluvium in the valleys is derived from both Palaeozoic greywackes and limestones (Gregg 1964). The whole region is mantled with loess deposited during the last glacial period (New Zealand Soil Bureau 1968).

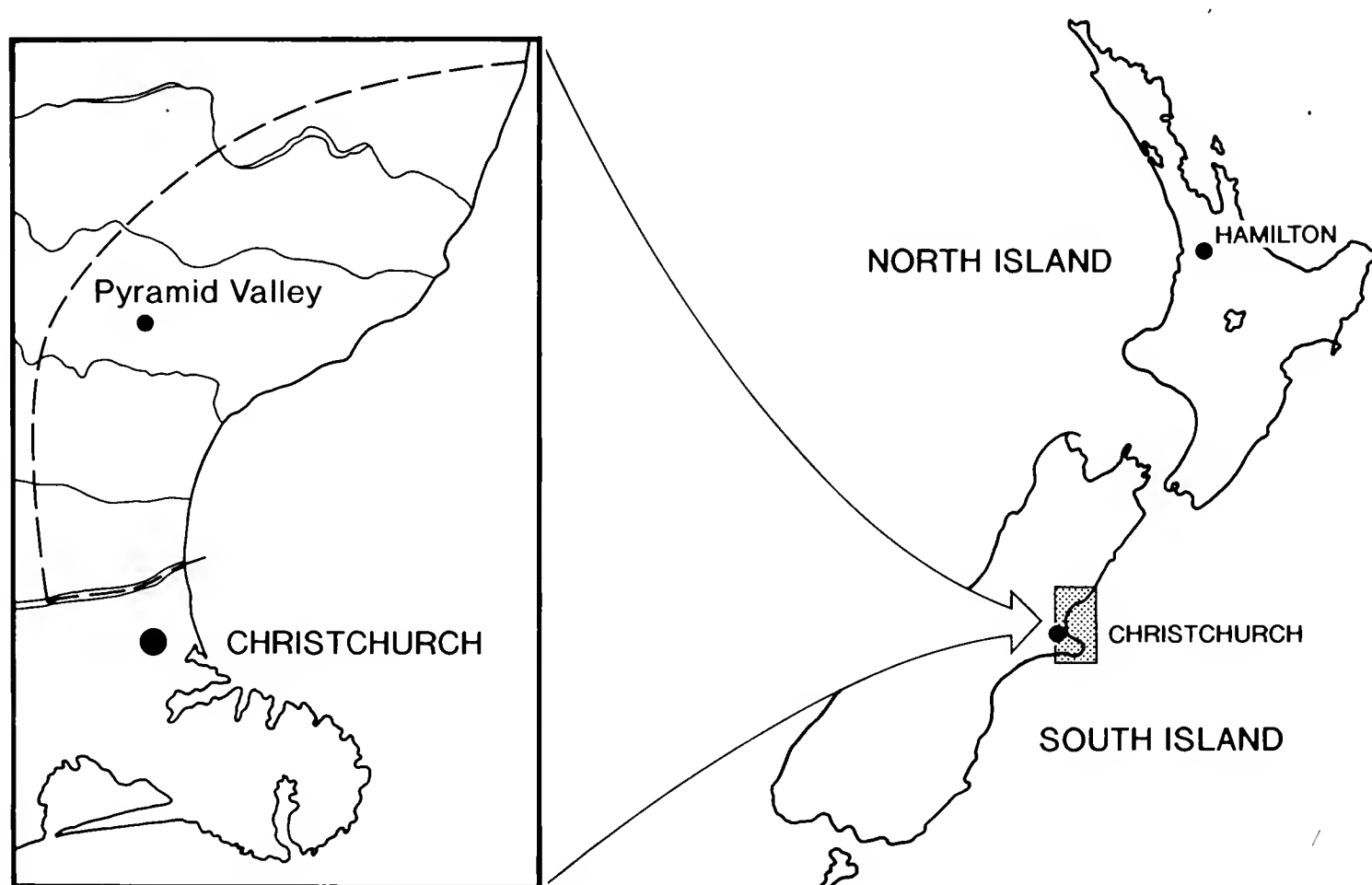


FIGURE 7 – Location of the North Canterbury habitat reconstruction region.

Soils in the region are southern yellow-grey earths weathered from loess and some limestone. Because rainfall is less than half that of the Waitomo region, soil leaching is reduced and base saturation is at a medium level. Soil pH is 5.7 and available phosphorus is low (New Zealand Soil Bureau 1968). More importantly North Canterbury, in common with many other parts of eastern South Island, is affected frequently by summer droughts.

Nature and age of the subfossil material

The subfossil bird bones recovered are mainly from alkaline swamps at Pyramid Valley (Falla 1941, Scarlett 1969), Glenmark and North Dean (Anderson 1989). Material from caves or rock shelters at Waikari (McCulloch 1975) and Weka Pass (Trotter 1972) are included as well as information from an earthflow at North Dean (Burrows et al. 1984).

Bird bones were accumulating at Pyramid Valley during the period 3740 to 2930 yr BP (Gregg 1972). A bone of *Pachyornis elephantopus* from Glenmark swamp gave a radiocarbon date of 2730 ± 70 yr BP (McCulloch & Trotter 1979). Two samples of bones of *Euryanas finschi* collected from the limestone cave at Waikari gave dates of 1920 ± 90 and 1080 ± 70 yr BP (McCulloch & Trotter 1979). Moa bone collected from the earthflow at North Dean gave a date of 1405 ± 50 yr BP (Burrows et al. 1984). The time span assumed for this reconstruction is c. 4000 to 1000 yr BP.

Swamps are not ideal places for preserving or recovering of small bird bones so it is likely that the avifaunal list compiled for this reconstruction is less complete than the others. Furthermore, in contrast to the Waitomo region, no information is available on the relative numbers of the smaller forest birds that were present.

Vegetation (Figure 8)

Matai-totara/mixed hardwood forest formed the pre-human forest cover; remains of the two conifers, matai and totara, are preserved as logs and seeds in various deposits, and their subfossil charcoal was mapped by Molloy et al. (1963). These two tall trees sometimes live in excess of 1000 years. The exact composition of hardwoods in the lower canopy is not clear as no remnants of this forest have survived. Kohuhu and mahoe are likely to have been important. These and other species listed in Table 14 have been included because they grow in similar sites elsewhere in North Canterbury, occur in neighbouring areas of comparable rainfall (Burrows 1969), or have been identified from gizzard contents recovered from the Pyramid Valley Swamp (Gregg 1972, Burrows 1989).

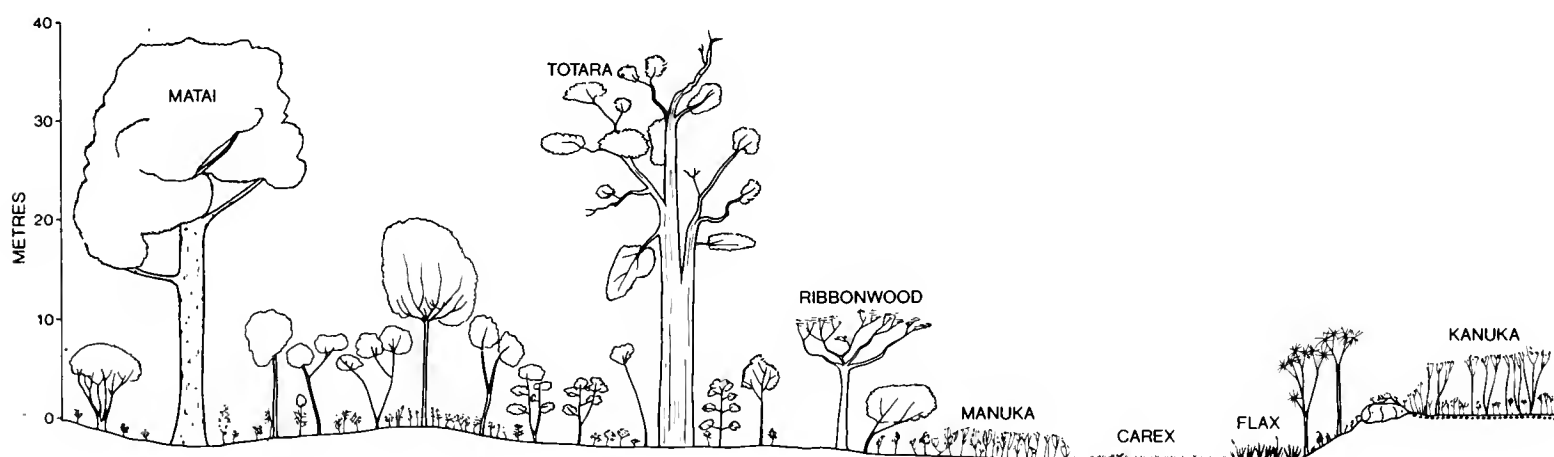


FIGURE 8 – Structure of pre-human conifer/hardwood forest in the North Canterbury region. The site includes poorly drained soils dominated by manuka, a swamp community dominated by *Carex secta* and flax *Phormium tenax*, and shallow stony soils dominated by kanuka. Scientific names of other plants given in Table 14.

The upper canopy of southern conifers was probably discontinuous except where young stands of these species were developing. In contrast to the forest described at Waitomo, this canopy was predominantly two-layered, with the crowns of the spaced conifers reaching 30 to 40 m height and greatly emergent above the lower canopy of mixed hardwoods at 8 to 15 m. Pokaka may have formed a discontinuous intermediate layer in some places. This forest could be described as “open” in its upper layers but because more light reaches lower levels in a two-layered canopy than one with three layers, the lower canopy and understorey were probably much denser than at Waitomo. The drier conditions and associated higher soil fertility would have favoured an abundance of small leaved shrubs, including those with tangled and interlaced

branching known as divaricating shrubs (Greenwood & Atkinson 1977). Epiphytes and tree ferns are unlikely to have been abundant and ground ferns, though common, would have been represented by fewer species than at Waitomo.

TABLE 14 – Major plant species of dry conifer/hardwood forest in the North Canterbury region.

Scientific name	Common name	Abundance ¹
CANOPY AND SUBCANOPY:		
Southern conifers		
<i>Podocarpus totara</i>	totara	c
<i>Prumnopitys taxifolia</i>	matai	c
<i>Dacrycarpus dacrydioides</i>	kahikatea	la
Hardwood trees		
<i>Cordyline australis</i>	cabbage tree	la
<i>Elaeocarpus hookerianus</i>	pokaka	a
<i>Lophomyrtus obcordata</i>		c
<i>Melicytus ramiflorus</i>	mahoe	a
<i>Myrsine australis</i>	mapou	a
<i>Pennantia corymbosa</i>	kaikomako	a
<i>Pittosporum eugenioides</i>	lemonwood	a
<i>P. tenuifolium</i>	kohuhu	a
<i>Plagianthus regius</i>	ribbonwood	a
<i>Pseudopanax arboreus</i>	fivefinger	a
<i>P. crassifolius</i>	lancewood	a
<i>Sophora microphylla</i>	kowhai	a
Woody lianes		
<i>Clematis paniculata</i>	clematis	a
<i>Muehlenbeckia australis</i>	pohuehue	a
<i>M. complexa</i>	small-leaved pohuehue	a
<i>Parsonsia capsularis</i>	NZ jasmine	a
<i>Passiflora tetrandra</i>	NZ passion-flower	c
<i>Rubus schmidelioides</i>	lawyer	a
<i>R. squarrosus</i>	lawyer	a
UPPER AND LOWER UNDERSTOREY:		
Hardwood trees and shrubs		
<i>C. crassifolia</i>		a
<i>C. linariifolia</i>		a
<i>C. lucida</i>	shiny karamu	a
<i>C. rhamnoides</i>		a
<i>C. rotundifolia</i>		c
<i>Corokia cotoneaster</i>		a
<i>Helichrysum aggregatum</i>		a
<i>Macropiper excelsum</i>	kawakawa	c
<i>Melicope simplex</i>		a
<i>Pseudopanax anomalus</i>		a
Juveniles of canopy and subcanopy trees		
GROUND STOREY:		
Shrubs		
<i>Coprosma rhamnoides</i>		a
<i>Macropiper excelsum</i>	kawakawa	a
Sedges		
<i>Carex</i> spp.		c
<i>Uncinia</i> spp.	hook grasses	c
Ferns		
<i>Asplenium gracillimum</i>		a
<i>Hypolepis ambigua</i>		c
<i>Phymatosorus diversifolium</i>		a
<i>Polystichum richardii</i>		c
¹ a = abundant species, present in 80% or more of stands		
la = locally abundant		
c = common species, present in 20-80% of stands		

At the time moas were becoming mired in the Pyramid Valley swamp, the vegetation there is likely to have been dominated by *Carex secta* with fringing stands of flax *Phormium tenax* (Moar 1970, Burrows 1989). Stands of manuka *Leptospermum scoparium* and *Myrsine divaricata* or *Olearia virgata* probably grew on poorly drained soils nearby together with some cabbage trees (Figure 8). Low forests of kanuka *Kunzea ericoides*, comparable to that described for Eyrewell Scientific Reserve by Molloy and Ives (1972), are likely to have covered the well drained very stony soils of stream terraces in the region.

Ground herbivores (Table 6, Figure 9)

Six species of moa are included in this guild; the smallest, *Emeus crassus*, was restricted to the eastern South Island and Stewart Island (Worthy 1990), and is the most common moa in both the Pyramid Valley and Glenmark swamps. Although little is known of its diet, this certainly included fruits of forest trees and shrubs (Falla 1941, Gregg 1972).

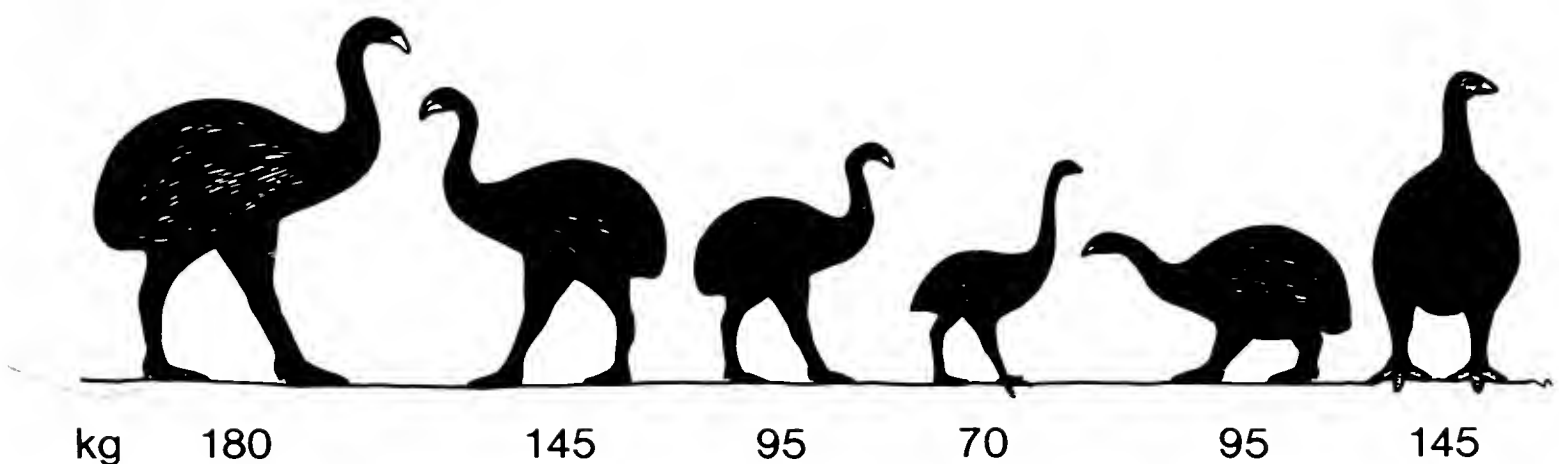


FIGURE 9 – Moas in the ground herbivore guild of North Canterbury. From left to right: *Dinornis giganteus*, *D. novaezealandiae*, *D. struthoides*, *Emeus crassus*, *Euryapteryx geranoides*, *Pachyornis elephantopus*. Estimated weights (kg) are shown for each species.

Euryapteryx geranoides were usually heavier birds than their conspecifics in the North Island, a general trend observed whenever a moa species is represented in both islands (Caughley 1977). Its relatively weaker mandible, compared with other similar sized moas, and small gizzard volume containing small stones (Worthy 1989) suggest it concentrated on foods of low-fibre content. How resources were partitioned with *E. crassus* is unclear; possibly one or other species was making greater use of open wetland habitats than forest but bones of both species were recorded from a forest environment in the North Dean earthflow dated between 1780 and 650 yr BP (Burrows et al. 1984).

Pachyornis elephantopus sometimes ate foods of such high fibre content as flax (Table 6), and may, therefore, have included swamp margins within its feeding range. However this does not indicate where it preferred to feed. Bones of this species were also recovered from the North Dean earthflow associated with the remains of matai forest (Burrows et al. 1984).

All three species of *Dinornis* were present in this guild but in the Pyramid Valley swamp the bones of *D. giganteus* were much more numerous than those of the other two species (Anderson 1989). It is doubtful whether the minimum number of individuals of moa species preserved in swamps gives a clear picture of their proportions in

forest. Some species may have preferred to feed in swamp margins. During the frequent severe droughts in the eastern South Island, moas may have been drawn to swamps in search of more succulent vegetation than that provided by an excessively dry forest or scrub understorey (Atkinson & Greenwood 1989). Water itself would probably not have been limiting because of the numerous large rivers in the region. Clearly, heavier animals, such as *D. giganteus* and *P. elephantopus*, would have a greater chance of becoming mired in a swamp, even if they were relatively uncommon in the forest itself.

That *D. giganteus* was using forest in the N. Canterbury region is demonstrated by the recovery of its bones (recorded as *D. maximus*) from a peaty deposit within forest dated between 1780 and 650 yr BP at the North Dean earthflow. The bones were associated with those of other forest animals including kiwi, Aptornis, Kakapo, Kaka and Tuatara (*Sphenodon* sp.) (Burrows et al. 1984).

Takahe bones have also been recovered from the Pyramid Valley swamp (Scarlett 1969) indicating their presence in North Canterbury in the late Holocene. Unlike at Waitomo, there is at present no evidence for their use of forest in North Canterbury. A similar reservation applies to Hodgen's Rail.

Two other ground herbivores present in the Pyramid Valley district were the Paradise Shelduck *Tadorna variegata* and the extinct South Island Goose *Cnemiornis calcitrans* (Scarlett 1969). Neither of these species are likely to have inhabited forest (Bisset 1976).

Arboreal herbivores, frugivore/herbivores and frugivore/nectivores (Table 7)

In species composition this guild is identical to that of the Waitomo region. However differences in the foods and feeding behaviour of North and South Island subspecies of Kokako are not known and therefore the relationship of the South Island Kokako to other birds in this guild may have been different.

Nectivores (Table 8)

Of the nectivore guild at Waitomo, only the Stitchbird did not occur in North Canterbury; this species is restricted to the North Island. Certain nectar sources important in the North Island example, for example rewarewa *Knightia excelsa* and northern rata *Metrosideros robusta*, were absent.

Aquatic insectivores (Table 9)

Brown Teal and Finsch's Duck were present in North Canterbury but bones of the Blue Duck have not been found. This may reflect the scarcity of fast-flowing streams and rapids in this lowland region.

Ground insectivores (Table 10)

With only five species recorded compared with seven from the Waitomo region, the structure of this guild may have been simpler in North Canterbury. One of the larger kiwis, most probably the Brown Kiwi but possibly the Great Spotted Kiwi *Apteryx haastii* was present. Bones of the Snipe-rail have not been found in the North Canterbury region and remains of the New Zealand Snipe are known only from Waikari cave (McCulloch 1975).

Of the surface-feeding ground insectivores, Wekas were present as well as the South Island Stout-legged Wren *Pachyplichas yaldwyni* (Millener 1988) and Robin. Bones of the Stephens Island Wren have not been recorded from the region.

Smaller arboreal insectivores (Table 11)

Five species only are recorded for this guild which includes the Brown Creeper *Mohoua novaeseelandiae*, a South Island endemic species, to some extent ecologically separated from remaining members of the guild by its habit of probing for invertebrates in holes and under bark on branches and twigs.

The Rifleman and Bush Wren are likely to have been present but have not been preserved in swamp deposits. The Whitehead is restricted to the North Island. Its South Island congener, the Yellowhead *Mohoua ochrocephala* is now largely restricted to beech *Nothofagus* spp. forests but this may not always have been the case.

Larger arboreal insectivores (Table 12)

The differences between this guild here and at Waitomo are small. The Huia is endemic to the North Island. The Long-tailed Cuckoo was not recorded, but its present widespread distribution in the South Island, and the occurrence of one of its main hosts, the Brown Creeper suggest that the apparent absence is likely to reflect circumstances unsuitable for deposition or preservation of bones.

The New Zealand Kingfisher *Halcyon sancta*, although now widespread in North Canterbury, is very poorly represented in subfossil deposits, suggesting a relatively recent even if pre-human arrival in the country (Millener 1981a, Turbott 1990). For this reason it is excluded from this guild in North Canterbury.

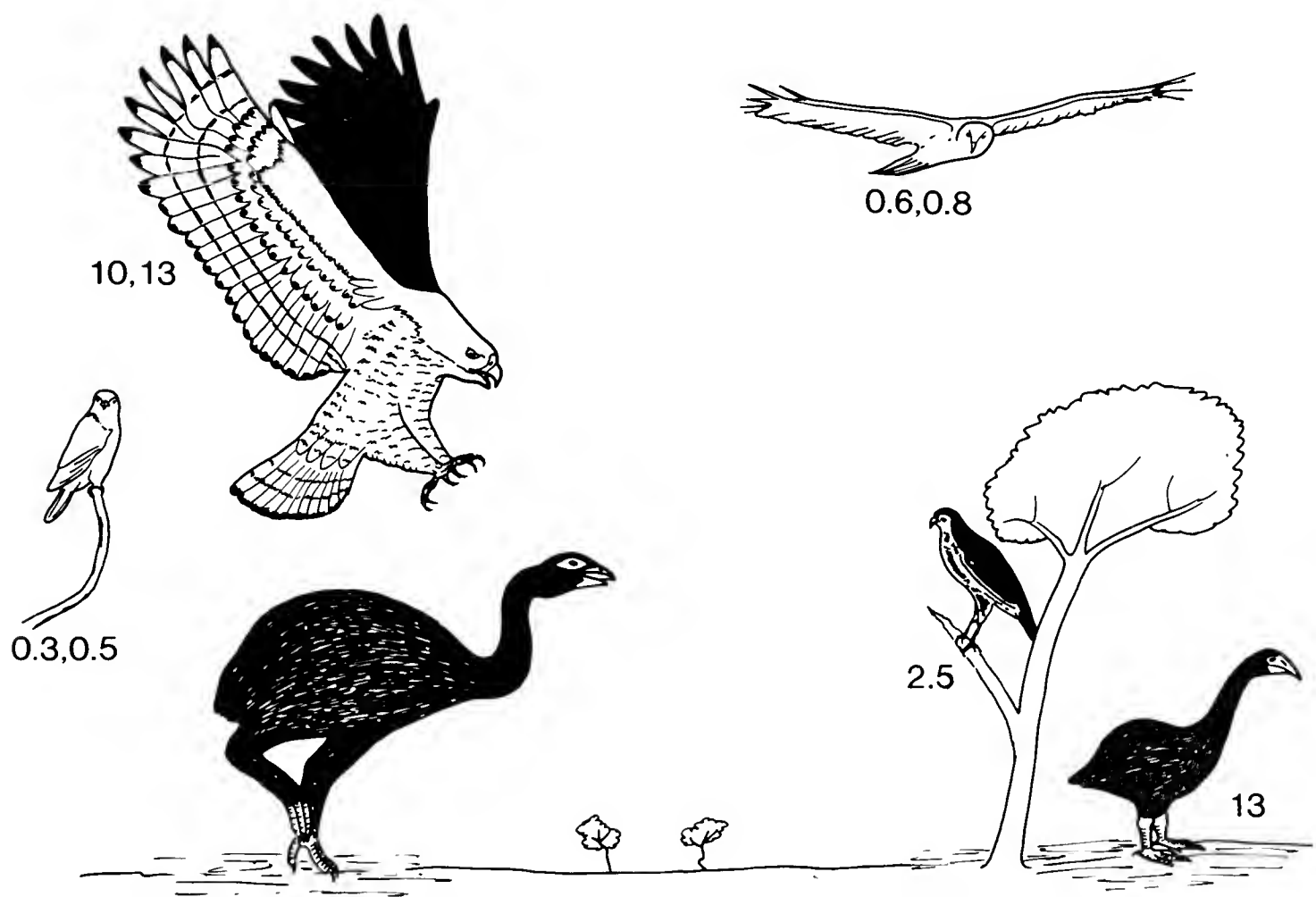


FIGURE 10 – Major predators of vertebrates in the North Canterbury region. From left to right: New Zealand Falcon, Haast's Eagle about to strike down a *Euryapteryx* moa, *Circus eylesi*, Harrier, and South Island Aptornis (bottom right). All weights in kg. Extinct species partly or wholly silhouetted.

Major predators of vertebrates (Table 13)

This guild is similar to that of the Waitomo region with an outstanding exception: the presence of the giant extinct New Zealand Eagle *Harpagornis moorei*, possibly the largest eagle that ever lived, with a wingspan of up to 3 m, talons as large as tiger's claws, and able to strike down full grown moas weighing from 100 to 250 kg. *Harpagornis* was a powerful flier which, although possibly too heavy to soar, would have swooped upon its prey from a high perch such as a tall tree or rocky bluff (Holdaway 1989; pers. comm).

Studies of the visual powers of the Australian Wedge-tailed Eagle *Aquila audax* by Reymond (1985) indicate that the vision of large raptors decreases more rapidly with failing light than is the case for man. This explains why most raptors do not hunt at or after twilight and may indicate that the moas were mostly if not all diurnal. In this case, predation by the New Zealand Eagle would have exerted strong selection pressure on moas to feed under cover of vegetation during daylight and only move to more open habitats at dawn or dusk.

No satisfactory explanation has been advanced for the apparent absence of *Harpagornis* from Holocene deposits in the North Island, a time period when most of this island was forest-covered.

The South Island Aptornis *A. defossor* has been recovered from at least two sites in N. Canterbury. It probably took the guild position of the North Island Aptornis but nothing is known about its feeding habits.

III. WARM TEMPERATE COASTAL FOREST ON DUNES

Site description

Areas of low sand dunes, from 10-200 m altitude, in the vicinities of North Cape and Cape Reinga in the far north of the North Island were chosen for this reconstruction. It will be referred to here as the "Northern Capes" region. These dunes are all of Holocene age but large blocks of basic volcanic rocks of Mesozoic age, as well as calcareous sandstones and siltstones of Tertiary age, flank the dunes (Kear & Hay 1961). Mean annual temperature varies between 15 and 17.5°C and annual rainfall from 1000 to 1400 mm, little more than half that for the Waitomo region. The soils are northern yellow-brown sands (Pinaki series) weathered from quartz sand with a pH of 5.6 and low available phosphorus (Cox 1977). Soil base saturation is in the high to medium range so that these soils are less leached of bases than those at other sites described.

Nature and age of the subfossil material

The dune area selected is the most northerly part of one of two major study areas used by Millener (1981a) in his analysis of the North Island's Quaternary avifauna. In this study subfossil bones were collected from eroding dune surfaces and deflation hollows with small-scale excavations to recover in situ material. These bones are largely natural deposits accumulated within forest (see below) although in some places shell-middens of younger age overlie and protect the older sands from erosion.

Dunes formed along most parts of the New Zealand coast only after sea level had reached its post-glacial peak some 6500 years ago (Schofield 1973, McLean 1978).

The oldest of 60 radiocarbon dates from dunes in the Aupouri Peninsula north of Kaitaia is 6040 ± 690 yr BP thus providing substantive evidence that dune development began only in the mid-Holocene. Forty-three of these dates are from material within the Northern Capes region and they span the age range 5380 ± 670 to 657 ± 32 yr BP (Millener 1981a). The time span for this reconstruction thus covers the period 6000 to 600 yr BP.

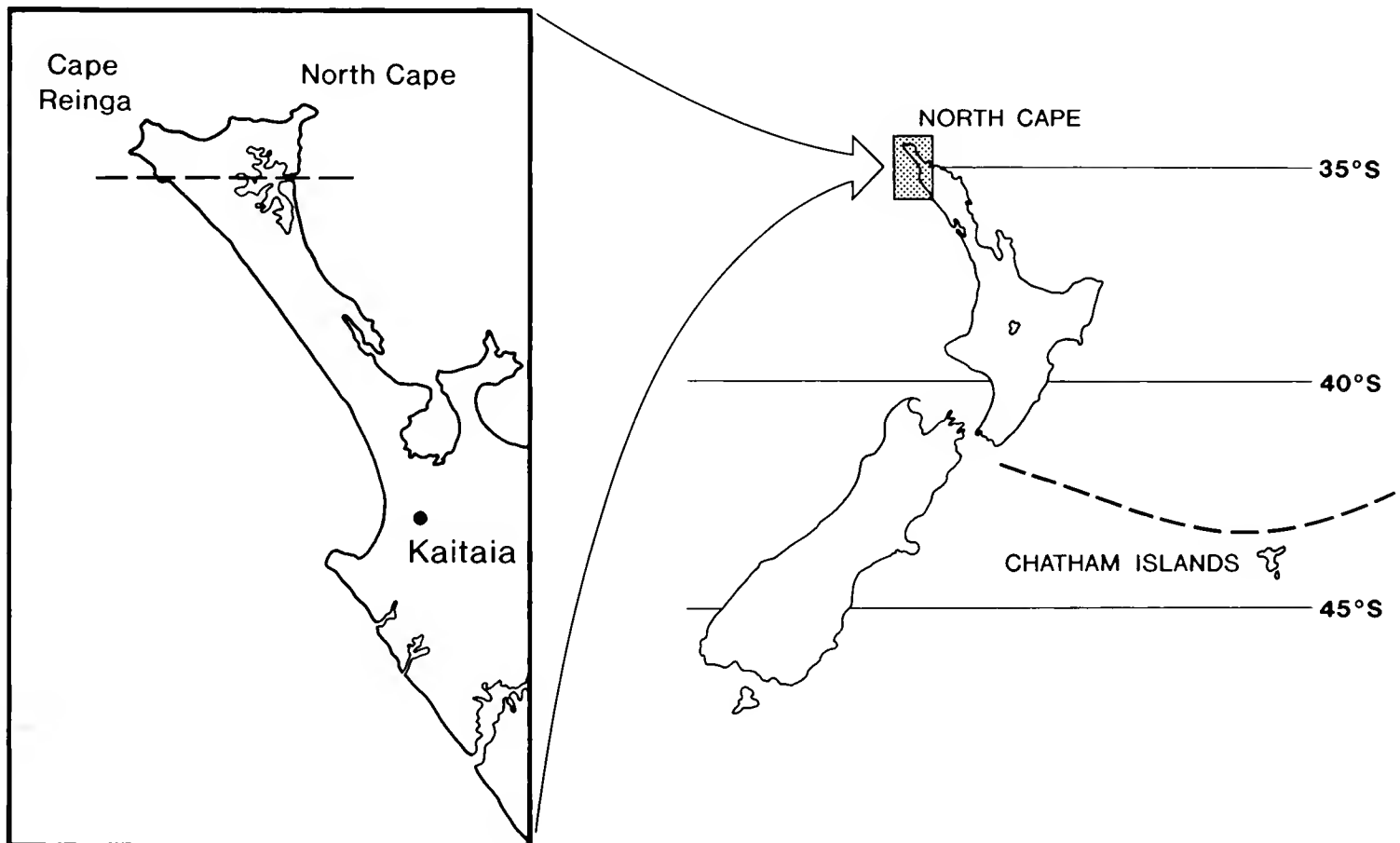


FIGURE 11 – Location of the Northern Capes habitat reconstruction region.

There is every indication that these dunes were covered in forest at the time the bones were deposited. All 30 species of landsnails found as subfossils within dune sites on the Aupouri Peninsula prefer forest, particularly accumulations of leaf-litter. Some species, e.g. *Serpho kivi*, are obligate arboreal snails. Most bird bones recovered are those of forest birds e.g. Kaka, two species of parakeet, Kokako, Pigeon, Tui and Saddleback (Millener 1981a). The rather uniform distribution in time of the radiocarbon dates suggests that these forest birds and other animals existed without major disruption throughout the 6000 to 600 yr BP period under discussion.

Earlier collections of subfossils on many of these dunes were biased towards moas but Millener (1981a) attempted to collect all material regardless of size; smaller species, particularly passerines, may still be under-represented. With this reservation, the composition of forest avifaunas derived from dune accumulations is considered more representative with respect to relative numbers than those derived from cave deposits.

Vegetation (Figure 12)

The pre-human forest of the Northern Capes dunes was a mosaic of pohutukawa forest on the younger dune soils, sometimes with kanuka, and rimu or totara/taraire-kohekohe-puriri forest on the older dune soils. Kauri *Agathis australis* forest was also certainly present on some older dune soils but is omitted from the discussion because there is little evidence of its association with the subfossil bone deposits. Stands of puriri/nikau, sometimes with supplejack, are likely to have filled some of the gullies.

There are virtually no remnants of this forest left to give a clear picture of its composition. Elsewhere along the North Auckland coast there are few remnants and even fewer adequate descriptions of dune forests. The remnant described very briefly by Gardner and Bartlett (1980) seems likely to be growing at least partly on sand. Thus the list of major species compiled for this mosaic forest (Table 15), is again a first approximation. This forest was more diverse in species composition than the other examples and contained several species not occurring as major components further south.

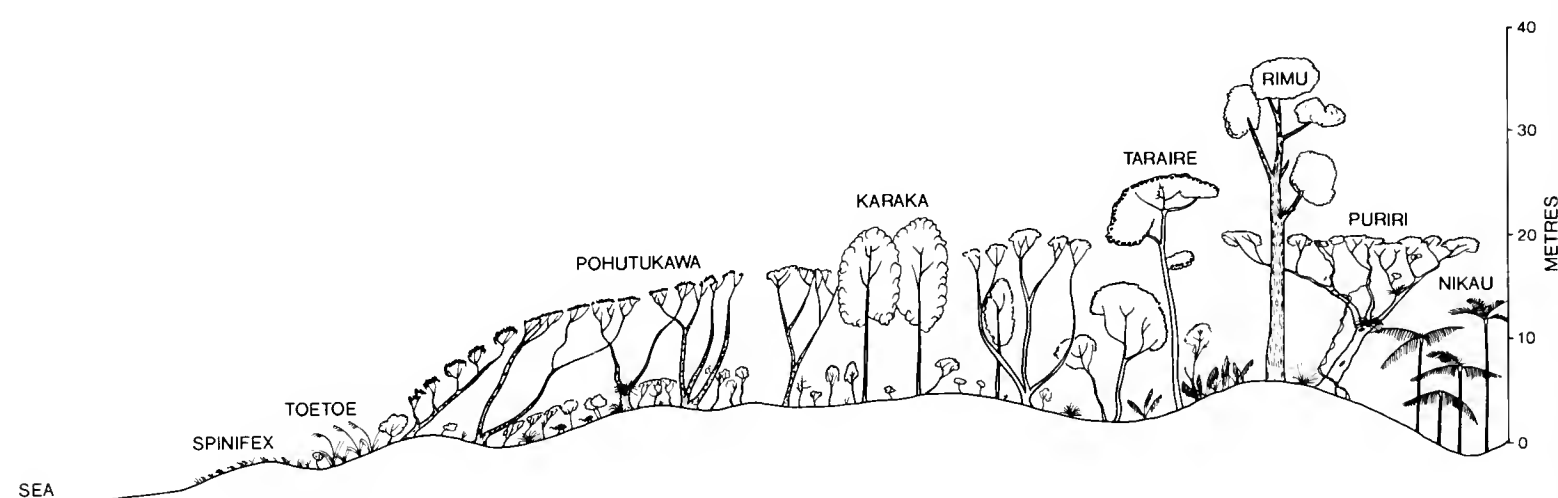


FIGURE 12 – Structure of pre-human coastal forest on dunes in the Northern Capes region. The pohutukawa canopy at left is clipped by wind-carried salt. Scientific names of plants given in Table 15.

The scattered emergent conifers probably formed only a very discontinuous upper layer so that the greater part of the canopy was one-layered in structure. Near the shoreline the canopy was reduced in height, a consequence of the effects of wind-carried salt. Mahoe and mapou would have been prominent in the relatively dense understorey. On the youngest dunes forest gave way to grasslands and sandfields of dune-toetoe *Cortaderia splendens*, spinifex *Spinifex hirsutus* and pingao *Desmoschoenus spiralis*.

Apart from the dune grasslands, other non-forest communities available to forest birds in this region included various wetlands in dune slacks and beside sand-entrapped lakes (such as Waitahora Lagoon and Waikuku Flat), and a variety of shrubland and scrub communities that had developed following lightning-induced fires or other major disturbance.

Ground herbivores (Table 6)

Although the same species of moa were present in this guild as in the Waitomo region, their proportions were different. The commonest moa at Waitomo, *Anomalopteryx didiformis*, was comparatively rare in the Northern Capes region. *Euryapteryx curtus*, with a minimum of 97 individuals from 15 of 18 sites examined, and *Pachyornis mappini*, with 64 individuals from 11 of 18 sites, are the most abundant moas in these deposits. *E. geranoides* was comparatively uncommon (found in six of 18 sites) (Millener 1981a).

The two largest species of *Dinornis* were again much less common than *D. struthoides* with bones of the latter being found more than twice as frequently as those of *D. giganteus*. Although open habitats were probably more available to moas in this region than at Waitomo, *D. giganteus* was still less common relative to the numbers

TABLE 15 – Major plant species of warm temperate coastal forest in the Northern Capes region.

Scientific name	Common name	Abundance ¹
CANOPY AND SUBCANOPY:		
Southern conifers		
<i>Dacrydium cupressinum</i>	rimu	c
<i>Podocarpus totara</i>	totara	c
Hardwood trees		
<i>Alectryon excelsus</i>	titoki	c
<i>Beilschmiedia tarairi</i>	taraire	a
<i>Carpodetus serratus</i>	putaputaweta	c
<i>Corynocarpus laevigatus</i>	karaka	a
<i>Dysoxylum spectabile</i>	kohekohe	a
<i>Elaeocarpus dentatus</i>	hinau	c
<i>Hoheria populnea</i>	hohere	c
<i>Kunzea ericoides</i>	kanuka	a
<i>Litsea calicaris</i>	mangaero	c
<i>Melicytus ramiflorus</i>	mahoe	c
<i>Metrosideros excelsa</i>	pohutukawa	a
<i>Myoporum laetum</i>	ngaio	c
<i>Myrsine australis</i>	mapou	a
<i>Pittosporum tenuifolium</i>	kohuhu	c
<i>Planchonella novo-zealandica</i>	tawapou	a
<i>Sophora microphylla</i>	kowhai	c
<i>Vitex lucens</i>	puriri	a
Monocot trees and other softwoods		
<i>Cordyline australis</i>	cabbage tree	la
<i>Entelea arborescens</i>	whau	la
<i>Rhopalostylis sapida</i>	nikau	la
Woody lianes		
<i>Muehlenbeckia complexa</i>	pohuehue	a
<i>Parsonsia capsularis</i>		c
<i>Ripogonum scandens</i>	suppiejack	c
<i>Rubus cissoides</i>	bush lawyer	c
UPPER AND LOWER UNDERSTOREY:		
Hardwood trees and shrubs		
<i>Brachyglottis repanda</i>	rangiora	a
<i>Coprosma arborea</i>		c
<i>C. macrocarpa</i>	coastal karamu	a
<i>C. parviflora</i>		c
<i>Macropiper excelsum</i>	kawakawa	a
<i>Melicytus ramiflorus</i>	mahoe	a
<i>Melicope ternata</i>	wharangi	c
<i>Rhabdothamnus solandri</i>	waiuatua	c
<i>Strelitzia heterophyllus</i>	turepo	c
Juveniles of canopy and subcanopy trees		
Tree ferns		
<i>Cyathea dealbata</i>	ponga	c
Epiphytes		
<i>Collospermum hastatum</i>	collospermum	c
<i>Griselinia lucida</i>	puka	c
GROUND STOREY:		
Shrubs		
<i>Coprosma rhamnoides</i>		a
<i>Macropiper excelsum</i>	kawakawa	a
Herbs, including sedges		
<i>Astelia banksii</i>	astelia	a
<i>Gahnia lacera</i>	cutty grass	c
Ferns		
<i>Asplenium oblongifolium</i>		a
<i>Doodia media</i>		a
<i>Phymatosorus diversifolium</i>		a
<i>Polystichum richardii</i>		c

¹a = abundant species, present in 80% or more of stands
la = locally abundant
c = common species, present in 20-80% of stands

of *D. struthoides* in the Northern Capes region than at Waitomo. This is consistent with *D. giganteus* being mainly a forest species in the North Island.

The only other ground herbivore was the Takahe with a minimum of 29 individuals recovered from nine of 18 sites Millener (1981a). If this figure for minimum number of individuals is scaled against that for *D. struthoides* (18 individuals) and the result compared with the equivalent figures for the Waitomo region, then Takahe were more than 2.5 times more common than *D. struthoides* in the Northern Capes region. This may reflect greater availability of swamp habitat and dune-toetoe grassland, or compositional differences in the forest itself.

Arboreal herbivores, frugivore/herbivores and frugivore/nectivores (Table 7)

Comparisons between the numbers of guild members can be made by using the minimum number of individuals (MNI) recovered by Millener (1981a) from 18 sites in the Northern Capes dunes. Kokako (MNI = 120 in 13 sites) were apparently nearly twice as abundant as Pigeons (MNI = 64 in 6 sites) and Kaka (MNI = 352 in 15 sites) more than 5 times more abundant than Pigeons. In the Northern Capes region Kakapo (MNI = 75 in 11 sites) were apparently as common as Pigeons whereas at Waitomo their remains were far more common, presumably because the flightless Kakapo became entrapped in caves more frequently.

Nectivores (Table 8)

The species composition of this guild was the same as that at Waitomo. If differences between sexes are averaged, body weights of guild members scale in the ratio of 3.9: 1.2: 1 for Tui, Stitchbird and Bellbird respectively. However in 18 sites examined, Bellbirds (MNI = 3 from 3 sites) and Stitchbirds (MNI = 1 from 1 site) occur infrequently in the dune deposits whereas Tuis (MNI = 54 from 4 sites) are more common (Millener 1981a). This probably reflects the greater chances of preservation for the Tui's larger bones. Given the abundance of Bellbirds in some coastal habitats last century before the establishment of numerous mammalian predators, it is probable that they were once common in these dune forests.

Aquatic insectivores (Table 9)

Only Brown Teal and Finsch's Duck were present as forest inhabitants although other ducks such as Grey Duck *Anas superciliosa*, Grey Teal *A. gracilis*, New Zealand Shoveler *A. rhynchos* and the extinct *Biziura delautouri* were all present in adjacent wetland habitats.

Ground insectivores (Table 10)

Three of the subsurface feeders of the Waitomo region were also present in the northern dune forests; the absence of the New Zealand Snipe can probably be attributed to poor conditions for preserving bones of this small bird. Although at Waitomo minimum numbers of Brown Kiwi exceeded Little Spotted Kiwis in a ratio of 1.8: 1, in the Northern Capes region the two species were present in equal numbers in the 18 sites examined: Brown Kiwi: 23 from 9 sites; Little Spotted Kiwi: 22 from 7 sites.

Wekas were very common in this northern region but of the three passerine surface feeders found at Waitomo, only the Robin was present. The absence of both the Stout-legged Wren and Stephens Island Wren could easily be a consequence of unsuitable conditions for preservation.

Smaller arboreal insectivores: < 50 g wt (Table 11)

Guild representation among the smaller arboreal insectivores is basically similar to that at Waitomo with the addition of Fernbirds *Bowdleria punctatus* and the absence of Rifleman and Tomtit. Fernbirds are likely to have used forest margins and scrub communities as well as forest. Rifleman may never have been common in coastal habitats of northern New Zealand.

Larger arboreal insectivores: < 50 g wt (Table 12, Figure 13)

The same guild of larger arboreal insectivores was found in the Northern Capes region as at Waitomo. The Kingfisher, now common in the region but again not present in subfossil deposits, has been included because this coastal zone would have offered suitable habitat for their establishment after arrival from Australia. To some extent their foraging may have overlapped with that of the Long-tailed Cuckoo but their feeding in aquatic and intertidal habitats probably provided sufficient ecological separation for them to establish and survive.

Despite its smaller size and presumably reduced chances of preservation in dune deposits, the Saddleback is much more numerous in these deposits than the considerably larger Huia. Turn-over of trees and shrubs in a coastal environment, providing a continuous supply of dead wood and small woodboring insects suitable for Saddlebacks, may have favoured this species in the manner suggested by Atkinson and Campbell (1966).

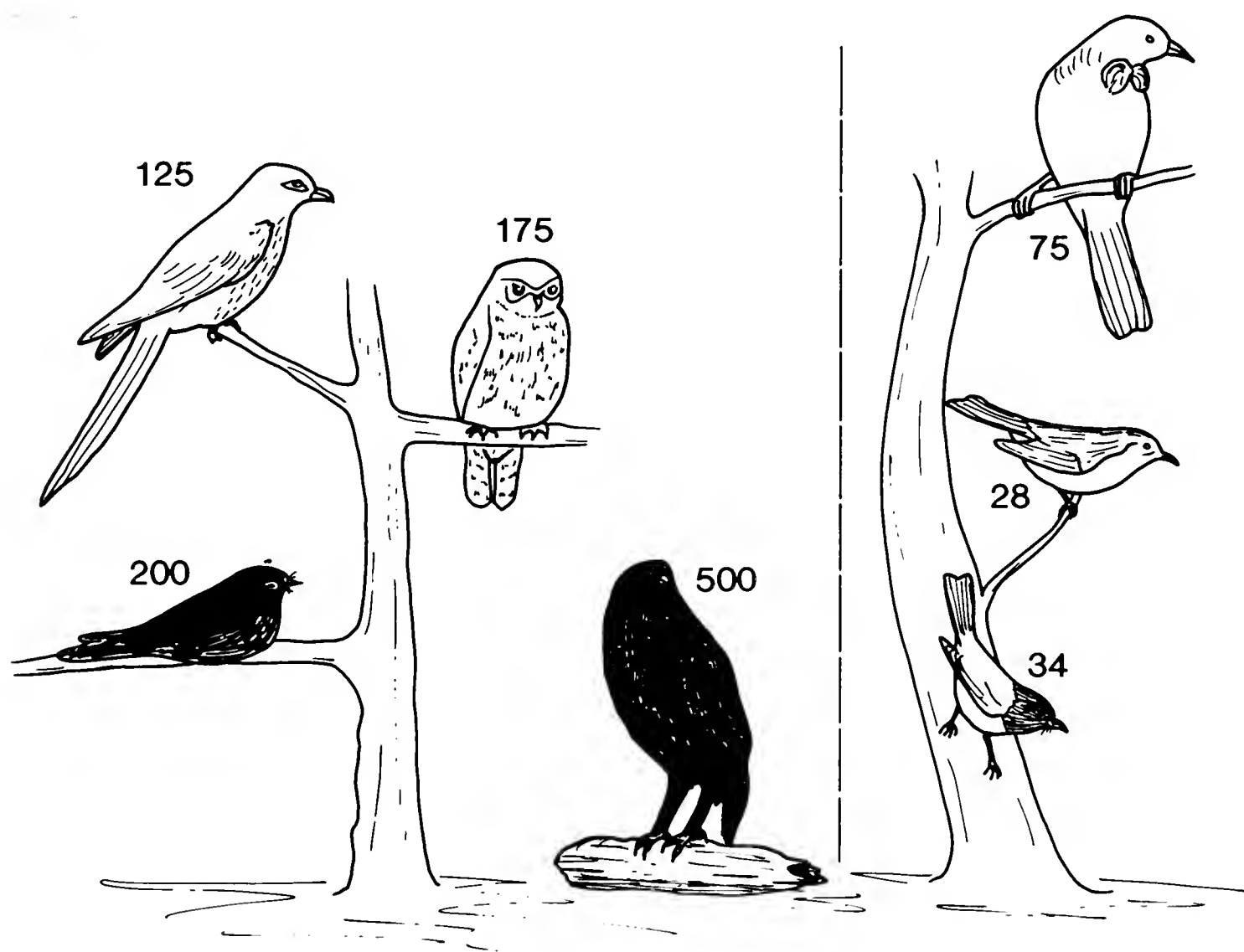


FIGURE 13 – Nocturnal arboreal insectivores (left) and members of the nectivore guild (right, drawn to larger scale). From left to right: Long-tailed Cuckoos (upper left), N.Z. Owlet-nightjar, Morepork, Laughing Owl, Stitchbird, Bellbird and Tui (top right). All weights in g. Extinct species silhouetted.

Of the two nocturnal raptors, bones of the Laughing Owl were recovered from 5 of 18 sites examined and of the Morepork, from 2 sites (Millener 1981a). The Piopio and Owlet-nightjar were also present but were not common.

Major predators of vertebrates (Table 13)

All four of the predators recorded at Waitomo were present in the northern region. Using the minimum number of individuals represented, the order of abundance was Harrier, Falcon, *Circus eylesi* and North Island Aptornis. The extinct New Zealand Crow *Palaeocorax moriorum* was apparently abundant and thus must have been a significant coastal scavenger.

Nesting seabirds

Although not deriving their food from within the dune forests, nesting seabirds, particularly burrowing petrels, are likely to have been significant in these forests, transferring nutrients such as nitrogen, phosphorus, calcium, potassium and magnesium from the sea to the land, particularly by excretion within and around burrows.

Subfossil bones of seabirds recovered from the dunes may have originated from those breeding ashore or from beach wrecks following storms. Among seabirds identified from these dunes, the Fluttering Shearwater *Puffinus gavia*, Little Shearwater *P. assimilis*, Fairy Prion *Pachyptila turtur* and Diving Petrel *Pelecanoides urinatrix* are most likely to have bred in the dune forest. At Tom Bowling Bay, a complete immature skeleton of *P. gavia* was found by Millener (1981a) in situ with a skeleton of *Euryapteryx curtus* dated at 2130 ± 30 yr BP. Remains of other animals found in the dunes included bones of an immature *P. urinatrix* associated with adult Tuatara bones within a fossil Tuatara/petrel burrow and also bones of immature Blue Penguins *Eudyptula minor*, a species that still breeds along this coast. Gannets *Morus serrator* may also have bred on some headlands.

IV. COOL TEMPERATE COASTAL FOREST ON BASALTIC HILLS AND VALLEYS OF CHATHAM ISLAND

Site description

This reconstruction is based on Chatham Island in the Chatham group, some 860 km east of Christchurch (Figure 14) and centres on the northerly aspect rolling hills and valleys east of Waitangi and south of Lake Huro and Te Whanga Lagoon, 10-100 m a.s.l. The basement rocks are Eocene tuffs (Red Bluff Tuff) which are fossiliferous and contain pillow lavas and lenses of limestone (Hay et al. 1970).

Mean annual temperature is about 11°C and annual rainfall varies between 625 and 1200 mm dropping as low as 500 mm in some years. Soils of the site area were mapped by Wright (1959) as brown granular loams and clays (Tiki brown clay and associated hill soils) from tuff, with a pH of 5.1 and medium base saturation and available soil phosphorus. Windrun in the Chatham Islands is very high with south-west winds predominating. When of low humidity these winds pick up large quantities of salt as aerosols from the sea which, in gale-force winds, is driven into the leaf tissue greatly retarding plant growth and modifying vegetation structure. A special feature of the Chatham environment is its proximity to the subtropical convergence of warm subtropical water with cooler subantarctic water (Figure 14). This zone of upwelling

and nutrient enrichment has resulted in the Chatham Islands becoming an exceedingly important site for breeding seabirds.

Marine transgression during the early Pleistocene appears to have largely inundated the Chatham region although a few small islands remained near the present summit of Chatham Island (Hay et al. 1970). Thus the present fauna and flora of these islands is likely to be composed mainly of transoceanic migrants from New Zealand, other oceanic islands, and Australia. Only a small fraction of the New Zealand biota has established in the intervening period and this isolation has resulted in development of a high level of endemism.

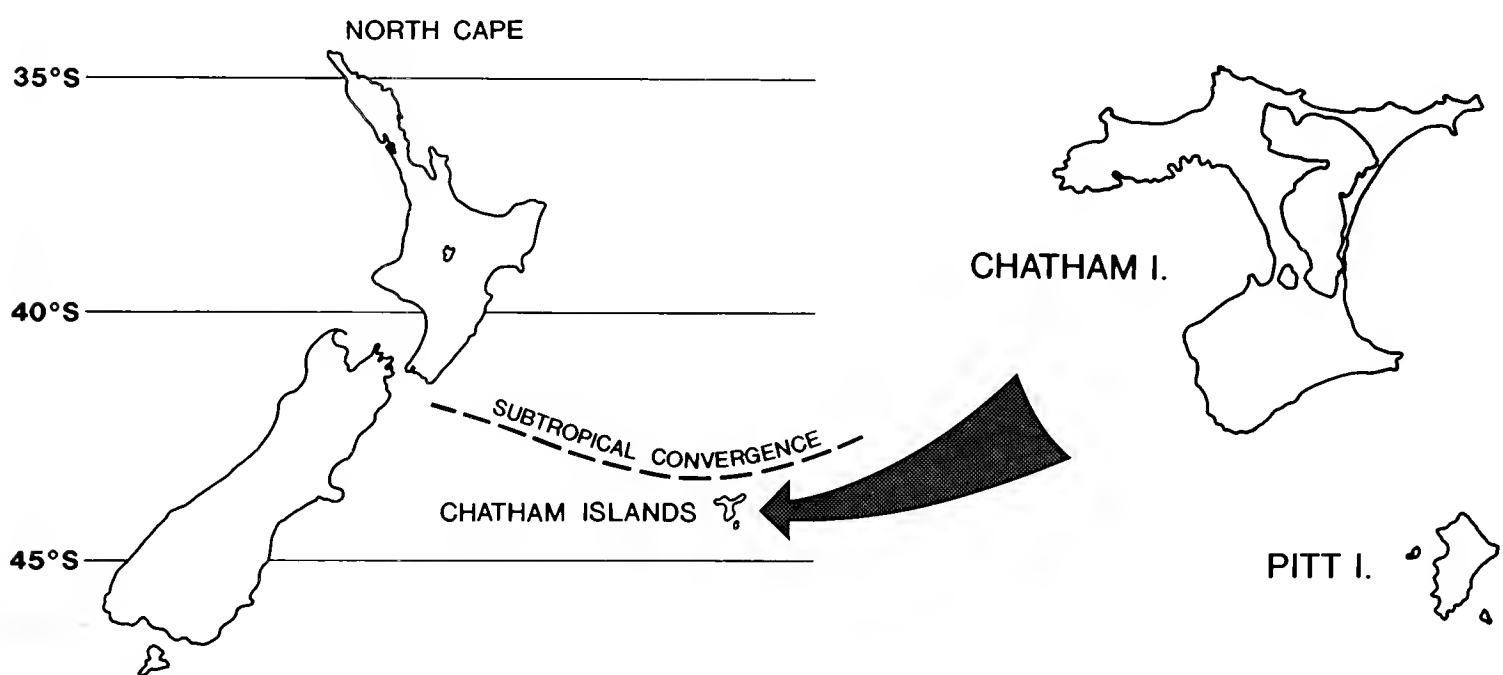


FIGURE 14 – Location of the Chatham Island habitat reconstruction and the position of the subtropical convergence.

Nature and age of the subfossil material

Knowledge of the pre-human avifauna of the Chatham Islands is derived primarily from bones found in dune deposits, particularly the dunes along the north coast and the west coast in Petre Bay between Lake Te Roto in the north and Waitangi in the south. These dunes have been searched intermittently by many collectors over a long period of time, the earliest scientific accounts being those of Forbes (1892a,b, 1893) and Rothschild (1907). More recent studies include those of Dawson (1957, 1959, 1960, 1961), Falla (1960), Bourne (1964, 1967), Olson (1984, 1990) and current studies by one of us (Millener 1980, 1981b).

We cannot be certain that these various collections have focused evenly on all species. Most bones have probably been collected from the dune surface or from cuttings exposed during wind erosion. As with the mainland, there is no evidence that these Holocene dunes began accumulating before the period of high sea level some 6500 years ago. We have assumed that this subfossil avifauna includes species that were important in Chatham Island coastal forest throughout most if not all the period 6500 to 1000 yr BP.

Information from subfossil deposits has been supplemented by studies of the extant avifauna or of birds that have become extinct only since contact with Europeans. These studies include those of Fleming (1939), Bell (1955), Dawson (1955), Lindsay et al. (1959), and many more recent observations by New Zealand Wildlife Service parties as well as those of the authors.

Vegetation (Figure 15)

The pre-human forest on these low volcanic hills and valleys was an akeake matipo - karamu forest in which ribbonwood and nikau were important at least locally (Table 16). Mahoe and kawakawa together with treeferns were likely to have been prominent in a moderately dense understorey. The ground storey would have been characterised by *Carex* sedges and many ferns including *Asplenium oblongifolium* and *Blechnum* spp. However where large colonies of burrowing seabirds were established, the undergrowth would have been very sparse with substantial areas of bare soil (Figure 15). Some information relating to this kind of forest can be derived from Wright (1959), Kelly (1983), and Given and Williams (1984)..

TABLE 16 – Major plant species of cool temperate coastal forest on Chatham Island.

Scientific name	Common name	Abundance ¹
CANOPY AND SUBCANOPY : Hardwoods and other trees		
<i>Coprosma chathamica</i>	karamu	a
<i>Corokia macrocarpa</i>		c
<i>Hebe barkeri</i>	koromiko	c
<i>Myoporum laetum</i> var.	ngaio	c
<i>Myrsine chathamica</i>	matipo	a
<i>Olearia traversii</i>	akeake	a
<i>Plagianthus regius</i> var. <i>chathamicus</i>	ribbonwood	c
<i>Pseudopanax chathamicus</i>	hoho	c
<i>Rhopalostylis sapida</i> var.	nikau	c
Woody lianes		
<i>Muehlenbeckia australis</i> var.	Chatham I. pohuehue	a
<i>Ripogonum scandens</i>	supplejack	c
UPPER AND LOWER UNDERSTOREY : Hardwood trees, shrubs and tree ferns		
<i>Cyathea dealbata</i>	ponga	c
<i>C. medullaris</i>	mamaku	c
<i>Dicksonia squarrosa</i>	wheki	c
<i>Hebe barkeri</i> x <i>H. dieffenbachii</i> (<i>H. "chathamica"</i>)	koromiko	c
<i>Macropiper excelsum</i>	kawakawa	a
<i>Melicytus chathamicus</i>	mahoe	a
GROUND STOREY ; Sedges ferns		
<i>Asplenium oblongifolium</i>		c
<i>Blechnum</i> spp.	hardferns	c
<i>Carex</i> spp.		a
¹ a = abundant species, present in 80% or more of stands. c = common species, present in 20-80% of stands.		

Karaka *Corynocarpus laevigatus*, known locally as kopi, is not included within the reconstruction. Its distribution in the Chatham Islands suggests that it had not occupied all possible habitats at the time of European arrival, an observation consistent with the strong tradition that it was introduced during settlement of the islands by the Moriori people.

This forest is quite distinct from those of mainland New Zealand. Nearly all the woody plants are endemic species or subspecies. Species diversity is highly restricted in all

layers of the forest, a consequence of the long isolation and relatively small flora of the Chatham Island group as a whole. The forest was of low stature seldom exceeding 20 m height and had a single-layered canopy with occasional emergent nikau; southern conifers are not native to the Chatham Islands.

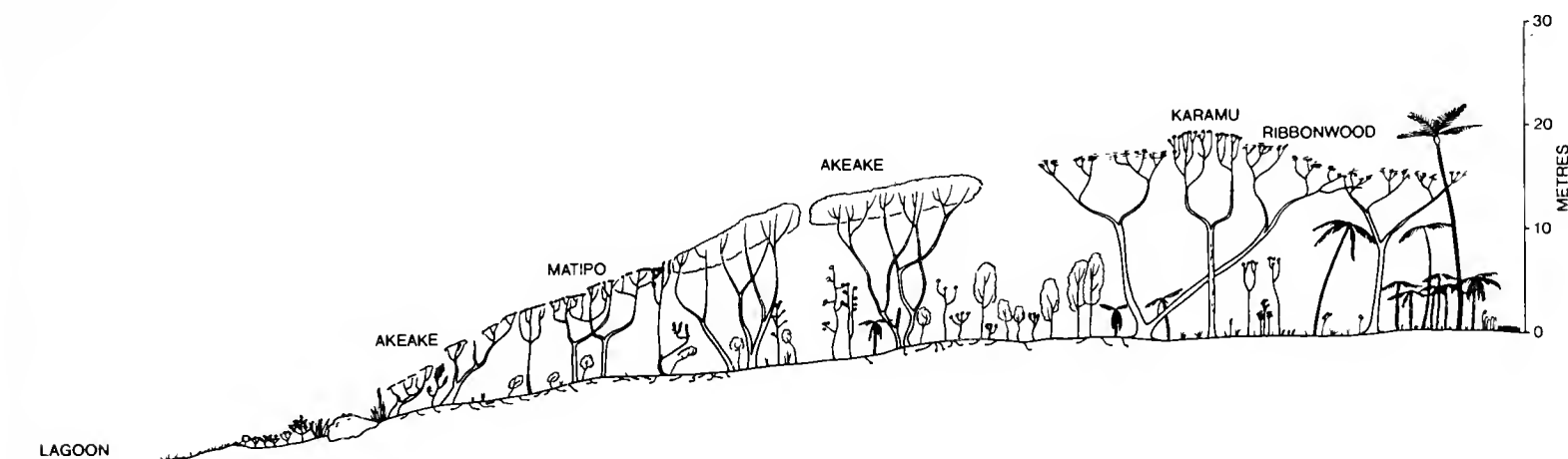


FIGURE 15 – Structure of pre-human coastal forest on low hills of the Chatham Island region. The akeake-matipo canopy at left is clipped by wind-carried salt. Numerous burrows of nesting petrels occupy parts of the forest floor. Scientific names of plants given in Table 16.

Ground and arboreal herbivores (Tables 6, 7)

Moas, Takahe, Kokako and Kakapo were absent from these guilds in the Chatham Islands. Consequently plant food sources may not have been as completely exploited as on the mainland but conversely the range of plant species was more limited.

The extinct Chatham Island Coot *Fulica chathamensis* was a heavier bird with longer legs than its mainland relative, the extinct New Zealand Coot *F. prisca* (Figure 16). It may therefore have been more terrestrial in its browsing or grazing, possibly responding to the lack of ground herbivores in the forest as well as to the absence of geese *Cnemiornis* spp. in the wetlands.

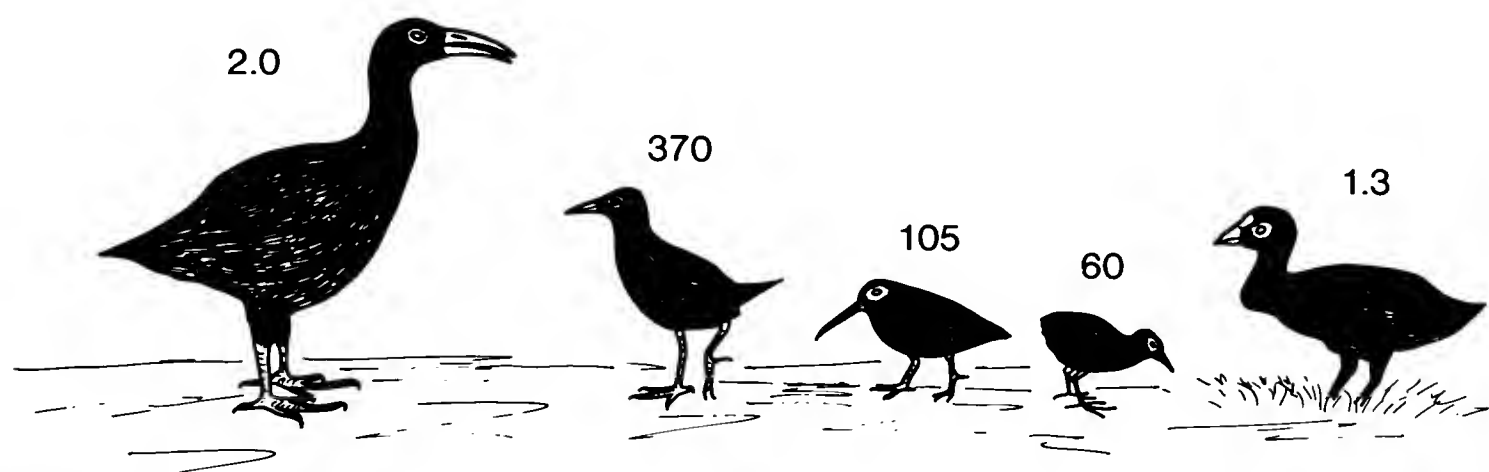


FIGURE 16 – The general insectivore guild in the Chatham Island region with a ground herbivore, the Chatham Island Coot, shown at far right. Other birds from left to right: Giant Chatham Island Rail, Dieffenbach's Rail, Chatham Island Snipe, Chatham Island Rail. Weights of three smallest birds in g, remainder in kg. All species shown are extinct. The extant Chatham Island Robin is not shown.

The reduced guild size of arboreal herbivores in the Chatham Islands may explain why bones of the Chatham Island Pigeon *Hemiphaga novaeseelandiae chathamensis* are found more frequently than any other forest bird in the dune deposits - without competition from birds such as Kokako and Kakapo, Pigeon numbers increased. The only

other arboreal herbivore was the Chatham Island Red-crowned Parakeet *Cyanoramphus novaezelandiae chathamensis* which has a more restricted diet than its mainland relative *C. n. novaezelandiae* (Table 7).

The feeding habits of the extinct Chatham Island Kaka are unknown. Like the extinct Norfolk Island Kaka *Nestor productus*, it had a longer and more pointed bill than that of the mainland Kaka, suggesting differences in feeding behaviour.

Nectivores (Table 8)

Only two members of this guild were present: the Bellbird and the Tui. The Chatham Island Bellbird *Anthornis melanura melanocephala* was substantially larger than its mainland relative *A. m. melanura* but nothing is known of its feeding habits. Apart from mahoe *Melicytus chathamicus* there are few nectar-producing plants that are common in these islands. This implies that the Tui's diet includes much less nectar than that of mainland populations.

Aquatic insectivores (Table 9)

The only representative of this guild was the Brown Teal which is now extinct in the Chatham group.

Ground insectivores (Table 10, Figure 16)

With five species this guild was rather more varied than those already discussed in the Chatham Islands. There were however no Kiwi, Snipe-rail, Weka or Wrens. All four of the original subsurface-feeding species are extinct. The smallest was the flightless Chatham Island Rail *Rallus modestus* which was at least partly nocturnal. The small size of its prey items and its semi-nocturnal behaviour may have helped it to coexist with the much larger Extinct Chatham Island Snipe *Coenocorypha chathamica* and Dieffenbach's Rail *R. dieffenbachii*. The extant Chatham Island Snipe *C. pusilla* had a shorter bill than *C. chathamica* and, contrary to the statement in Turbott (1990) is not "abundant in subfossil and midden deposits"; so far it has not been recovered from subfossil deposits and may indeed be a comparatively recent immigrant.

Dieffenbach's Rail was twice as heavy as the Banded Rail *R. phillippensis* and had a reduced keel and shorter wings compared with the mainland species. Together with the Giant Chatham Island Rail *Diaphorapteryx hawkinsi*, it may have taken the place of the Weka, bones of which have not been recovered as subfossils from the Chatham Islands, notwithstanding the comment by Fleming (1939: 493). The Giant Rail was more than twice the body weight of a Weka and the greater curvature of the bill may suggest it was somewhat less predatory in habits. However, considering the vast concentrations of seabirds once present on Chatham Island, it would be surprising if neither the Giant Rail nor Dieffenbach's Rail preyed on petrel chicks or even adult birds.

The smallest member of this guild was the Black Robin *Petroica traversi* which feeds both on the ground and in the lower understorey. It remains as the sole survivor of the original ground insectivore guild in the Chatham Islands.

Arboreal insectivores (Tables 11,12)

Of the smaller arboreal insectivores, five are represented on Chatham Island: the Tomtit, Fantail, Chatham Island Warbler *Gerygone albofrontata*, Shining Cuckoo and

Chatham Island Fernbird *Bowdleria rufescens*. Their differing habits ensured little overlap in foods taken. The Chatham Island Warbler spends more of its time glean-ing from trunks and branches than its mainland relative, perhaps because the three species that feed from these stations on the mainland are absent: Rifleman, Brown Creeper and Saddleback. The extent to which the extinct Chatham Island Fernbird used forest or forest margins is not known.

The only larger arboreal insectivore present was Forbes' parakeet *Cyanoramphus forbesi* which has developed insectivorous behaviour sufficient to separate it ecologi-cally from its closest relative, the Chatham Island Red-crowned Parakeet.

Major predators of vertebrates (Table 13)

Although the sizes of most feeding guilds in the Chatham Islands are reduced rela-tive to those of the mainland, the predator guild was an exception. It contained at least four species which, in order of increasing size were the N.Z. Falcon, Harrier, Brown Skua *Catharacta skua* and the Extinct Chatham Island Sea Eagle *Haliaeetus australis*. Only the Harrier and Skua have survived. The Giant Rail was also possibly a preda-tor of vertebrates.

The Falcon probably ate a range of the smaller forest birds; the Harrier could have supplemented its diet of passerine birds and insects with seabird carrion or by prey-ing on small or young seabirds, as Brown Skuas do today (Table 13). The Sea Ea-gle, from which only very limited material has been recovered, could have preyed on the waterbirds common on the island's extensive network of lagoons and lakes as well as taking larger seabirds such as the taiko *Pterodroma magentae* and Sooty Shearwater *Puffinus griseus*, in addition to fish.

As in the Northern Capes coastal region the extinct New Zealand Crow was common, perhaps reflecting the extensive coastal and lagoon shorelines where carrion or prey could be found.

Nesting seabirds

The large seabird colonies were concentrated on the brown granular clays and loams, and the yellow brown sands of the coastal zone, soils which would have been mod-erately easy to burrow although sandy soils under forest are likely to have been a preferred substrate for the smallest petrels. These volcanic and sandy soils contrast with the widespread peat soils of the interior of Chatham Island where burrowing was probably rare owing to high water tables. Within this zone (which extends well beyond the area of this reconstruction), the subfossil bone deposits indicate that four seabirds were very abundant in the past: the Taiko, which was broadly distributed, the Broad-billed Prion *Pachytila vittata*, the White-faced Storm-petrel *Pelagodroma marina maoriana* present in huge numbers in places, and the Common Diving Petrel *Pelecanoides u. urinatrix*. Seabirds whose burrows were more localised in distribution, but nevertheless very common, were Sooty Shearwater, Chatham Petrel *Pterodroma axillaris* and Fairy Prion *Pachyptila turtur*. Blue Penguins were also common and a species of Crested Penguin *Eudyptes* sp. was locally common.

Extrapolating from the Snares islands (Warham & Wilson 1982), the total seabird population of Chatham Island would have totalled many millions of birds. The quan-titative effects of such a vast transfer of nutrients from the sea in promoting plant growth and influencing vegetation development, must have been very significant.

GENERAL DISCUSSION

Partitioning of food resources

A major goal of this study has been to understand how food resources available to birds in lowland forests could have been partitioned between co-existing species in the past. The approach taken, through guilds, must necessarily be qualitative until such time as additional data become available.

Food partitioning among the ground herbivores is least clear because of the many extinct species (Table 17). Some possible mechanisms for partitioning have been identified that deserve further study. These include a body size/gizzard weight/food quality relationship, hindgut modifications for fermentative digestion, height differences between species, differences in bill shape and musculature, and inclusion of animals in the diet.

TABLE 17 – Numbers of bird species in pre-human forest feeding guilds.

Forest guild	No. of species in reconstructed habitats (Bracketed nos = extant species ¹)			
	Waltomo	North Canterbury	Northern Capes	Chatham Island
Ground herbivores	9(1)	9(1)	8(1)	1(0)
Arboreal herbivores + frugivore/ herbivores	5(5)	5(5)	5(5)	2(2)
Frugivore/insectivores	1(1)	1(1)	1(1)	1(1)
Nectivores	3(3)	2(2)	3(3)	2(2)
Aquatic insectivores	3(2)	2(2)	2(2)	1(1)
Ground insectivores	8(5)	5(4)	5(4)	5(1)
Smaller arboreal insectivores	7(6)	5(5)	6(5)	5(4)
Larger arboreal insectivores	7(3)	5(2)	8(4)	1(1)
Major predators of vertebrates	4(2)	5(2)	4(2)	4(3)
Carrion feeders	1(0)	1(0)	1(0)	1(0)
Totals	48(28)	40(24)	43(27)	23(15)
% losses from species extinctions ²	42	40	37	35

¹ Species still extant may be locally extinct in the area of the reconstructed habitat but have survived elsewhere in the New Zealand region, sometimes as a different subspecies.

² For the reason that not all species originally present in a particular reconstructed pre-human habitat have yet been found in subfossil deposits, these extinction figures indicate the *minimum* losses that have occurred.

Partitioning of available food between species among the arboreal herbivore, frugivore/herbivore, frugivore/insectivore, nectivore and aquatic insectivore guilds do not pose major problems of interpretation. Among the ground insectivores, the sub-surface feeders are clearly differentiated by body weight and bill length, and thus by implication, foods taken. However the differences in feeding behaviour among the

small passerines of this guild are not clear; nor how they divide food with passerine arboreal insectivores that feed in the ground storey or lower understorey. The probability is that some of these birds were feeding on similar foods but at different feeding sites in the manner described by Gibb (1961) and Moeed and Fitzgerald (1982).

Partitioning of food between birds in the remaining guilds is understandable in terms of their morphology, body weights and likely feeding behaviour except that the trophic position of *Aptornis* is not known with any certainty.

The use of different forest strata is seen as a major factor associated not only with different feeding guilds but also with separation of species within the same guild. Similar findings have been reported in previous studies such as that of Holmes and Recher (1986). However, a limitation of the present analysis is that lack of knowledge of the social behaviour, seasonal migrations and size/density relationships of extinct species, has prevented assessment of their importance in food partitioning and species co-existence.

Similarity of feeding guilds in mainland lowland forest

The three mainland habitat reconstructions differ markedly in climate, rock type and soils, and particularly in structure and floristic composition of the forest. Yet the species composition of their feeding guilds is remarkably similar. Of the 56 mainland species listed in Tables 6-13, 31(55%) are common to all three reconstructions and a further 13 (23%) occur in two. These figures underestimate the degree of commonality because several species likely to have been present in one or more of the reconstruction regions were not found as subfossils.

The largest differences relate to the absence from North Canterbury of seven species restricted to the North Island, and the absence from the two North Island examples of five species restricted to the South Island. In two cases, the Stout-legged Wrens and *Aptornis*, we have apparently pairs of ecologically equivalent species. Differences in guild composition are thus considerably a consequence of biogeographic history rather than reflecting environmental differences.

In view of the importance of forest stratification in facilitating ecological separation of species, it is of interest that differences in canopy structure appear to have had little influence on guild composition. The three mainland reconstructions vary from a full three-layered canopy (reconstruction I) through the two-layered canopy of II to the almost single layered canopy of the Northern Capes reconstruction (III); yet the numbers of bird species in each guild are little different (Table 17). Small differences, as between reconstructions I and III for example, may be more apparent than real as a result of poorer preservation of very small birds in dune deposits compared with cave deposits.

Other collections of subfossil bird bones from both natural and midden sites in the lowlands suggest a high degree of co-existence of species. The general conclusion seems warranted that evolution in New Zealand's lowland avifauna has favoured adaptations allowing birds to use the same basic food source in the same forest habitat but in different ways. It has not favoured differing avifaunas and guild structures associated with different kinds of lowland or coastal forest.

This conclusion is based largely on qualitative data. When sufficient information becomes available to compare the avifaunas and guild structures of lowland kauri or beech forests with the more widespread types of lowland and coastal forest described here, it is likely that quantitative differences in avifaunas and guild structures will be evident.

The Chatham Island forest-bird system

The outstanding feature of this system is the paucity of species in some guilds. The ground herbivore, arboreal herbivore, frugivore/herbivore and larger arboreal insectivore guilds were either almost non-existent or had very few species, perhaps a consequence of the restricted flora of the Chatham Islands. However, plant productivity is likely to have been high in this system, even allowing for the effects of salt, as a result of nutrient input by seabirds. Plant species diversity was probably not a factor limiting avian diversity, especially as some feeding guilds are of comparable size to those of the mainland (Table 17). The long geographical isolation of the Chatham Islands, which precluded colonization by less mobile bird species, is more likely to be the correct explanation.

The gaps in guild structure seen in the Chatham Island system are of great interest from an evolutionary standpoint. Some birds that have colonised these islands have, in the absence of certain competitors, had a wider range of foods available. Although many species when compared with mainland relatives (see text), show size increases (Appendix 1), differences in bill proportions and behavioural changes, their possible diet extensions are poorly documented.

Flightlessness and nocturnal activity in New Zealand forest birds

Twenty-two (33%) of the 67 species listed in Tables 6 to 13, including both forest inhabitants and species that made major use of the forest, were flightless. A further six species (9%) showed reduced powers of flight. This conforms with the very high incidence of reduced capability for flying seen in the terrestrial avifauna as a whole (Bell 1991) and presumably reflects both the absence of mammalian predators and opportunities provided by forest to escape from avian predators.

Many forest birds were also active at night; 14 (21%) of the 67 species were either nocturnal or fed both by night and day. Among the 23 species of the ground insectivore and larger arboreal insectivore guilds, at least 11 showed nocturnal activity (Tables 10, 12). Eisenberg (1981) has commented that diurnal insectivores, frugivores and nectivores are generally birds while at night these roles are taken by mammals. Evidently, yet another effect of the lack of indigenous terrestrial mammals in New Zealand has been to increase opportunities for nocturnal foraging among birds.

Thus evolutionary responses by New Zealand birds to the absence of mammals include both those relating to mammals as predators and those where mammals act as competitors.

Comparison of forest avian guilds in New Zealand with equivalent guilds overseas

The guild of flightless forest herbivores dominated by the moas had no equivalent among birds elsewhere, although the extinct elephant birds (*Aepyornis*, *Mullerornis*) of Madagascar deserve comparison. The array of extinct geese now known from Hawaii (Olson & James 1982) show some similarities but were probably not forest

birds. Where ratites, usually only one species, occur in other countries they invariably co-exist with herbivorous mammals. In Madagascar, 12 species of ratite have been identified from subfossil deposits (Battistini & Verin 1972). Their forest habitat has been largely destroyed but it is possible that co-existence of species occurred within forest as in the case of the moas. The major mammalian herbivores there were arboreal lemurs which co-existed with both elephant birds and giant tortoises. Thus as in New Zealand forests, the guild of ground herbivores is likely to have developed primarily because mammalian herbivores were absent, particularly those that feed in the lower understorey.

Although New Zealand's ground herbivores can be compared with African herbivore systems, there are important differences. The much greater diversity and concentrations of African browsing mammals are associated with savanna woodlands rather than forest. The most distinctive feature of the New Zealand guild was its dependence on forest in many parts of the country. We have at present no real evidence that moas were flocking species.

Where ground herbivore guilds occur elsewhere, the animals concerned are usually small-bodied ungulates, such as the forest duikers of equatorial Africa or the brocket deer of Amazonia. Because new leaf growth and fruit in a forest are concentrated in the upper layers, these animals have often become more omnivorous by supplementing their diet with animals (Bodmer 1989).

With arboreal herbivores elsewhere, the number of birds that are obligate folivores in forest may total as few as four species; extraction of energy from leaves requires a longer retention time in the alimentary canal which in turn necessitates large storage space and increased body weight (Morton 1978). Since flight requires rapid extraction of energy, arboreal folivory is uncommon in flying birds though important in primates. No New Zealand arboreal bird eats leaves as a sole food but four or five species use leaves as a major food (Table 7) making this guild unique. Quantitative data are lacking, but the three larger arboreal frugivore/herbivores were probably once all common. The absence of arboreal mammalian herbivores, particularly folivorous primates, some marsupials and rodents, and sloths, probably facilitated the development of this guild.

Many New Zealand forest birds eat fruit; even most insectivores take some fruit, particularly in winter (cf. O'Donnell & Dilks 1989b). But only three or four of the 67 species included in this study, either frugivore/herbivores or frugivore/insectivores are usually if not always dependent on fruit for successful breeding (Table 7). This contrasts with the diversity of the frugivore guild in tropical forests where a greater variety of fruit is available year-round and where parrots, pigeons, manakins and hornbills are adapted to a partly or wholly frugivorous diet, e.g. the fruit pigeons of tropical Queensland (Chome 1975).

The nectivore guild in New Zealand has few species and none are solely dependent on nectar. This contrasts again with tropical forest but presumably reflects the rather restricted range of nectar sources available.

The subsurface-feeding group of ground insectivores is unusual and has no avian counterpart in forests elsewhere. Feeding by kiwis on large subsurface invertebrates

can be considered as partly equivalent to that of some fossorial mammals such as moles.

Lein (1972) has commented on the paucity of ground-feeding insectivorous birds in Australia, suggesting their replacement by the large number of marsupial insectivores and lizards. Although New Zealand had no marsupials, groundfeeding insectivorous birds would certainly have been competing with species of lizard that were present at high densities.

Considering the two groups of arboreal insectivores as a single guild, it is the largest of any described. The 14 mainland members include representatives of 12 different bird families. It is limited in species diversity when compared with equivalent guilds of the continental tropics, e.g. Croxall (1977) found up to 50 passerine insectivores co-existing in New Guinea rain forest. When compared with temperate continental forests, however, the restriction of species is no greater than might be expected from the much smaller land area of New Zealand. Thus Terborgh & Robinson (1986) recorded 25 species in the arboreal insectivore guild of a lowland temperate forest in South Carolina, U.S.A. Five of these were woodpeckers. In New Zealand the two insectivorous wattlebirds, Huia and Saddleback, had to some extent adopted the trophic role of woodpeckers (Table 12).

The guild of major predators of vertebrates appears to have been capable of coping with the complete size range of terrestrial vertebrates present. This underlines a fact stressed by Holdaway (1989): "New Zealand's avifauna did *not* evolve in the absence of predators but only in the absence of *mammalian* predators". Thus behavioral and morphological adaptations for avoiding avian predators should be expected in the New Zealand land fauna, both invertebrate and vertebrate. For example, the cryptic green, yellow and brown plumage of the nocturnal Kakapo cannot be understood unless it is known that this parrot frequently roosts during the day in shrubs or small trees. There it was once vulnerable to *Circus eylesi* and the New Zealand Eagle. Diamond (1990) discusses further examples.

Predators are sometimes effective controlling agents in communities of large mammals both in Africa and elsewhere (Lawton & MacGarvin 1986, Diamond 1986). Whether the eagle sometimes limited the density of moa populations, or whether *Circus eylesi* exerted a controlling influence through predation on moa chicks, are questions still to be answered.

Although there is little comparable data from other countries, the lowland forest of the New Zealand mainland described here, with 56 bird species distributed in 10 guilds, is similar in birds species diversity and guild structure to at least some continental systems. For example, a multi-tiered virgin forest in the temperate lowlands of South Carolina, U.S.A., studied by Terborgh and Robinson (1986), supported 40 species, also in 10 guilds using the same guild criteria. Factors additional to land area and degree of isolation will need to be considered before the composition of forest-bird systems in New Zealand is properly understood.

Forest/bird systems of the past in relation to those of the future

How can an improved understanding of these past systems assist with better management of present and future systems? Appreciating what we have lost may strengthen our resolve to protect what we have left. But limiting our management strategies solely

to those of protection will deny us opportunities for restoring some systems. To talk of recreating the pristine state is unrealistic. But to talk of extending the range of forest/bird systems beyond those we have, as well as increasing the diversity of some existing systems, is realistic. Extinctions among New Zealand plants are few so that it is the animal part of the system where the real challenge lies.

At least 40% of the bird species originally present in these systems are extinct (Table 17). The ground herbivore, ground insectivore, larger arboreal insectivore and major predator guilds have suffered the greatest losses and scope for restoring these is very limited. In special situations, extant species having a similar trophic role to those extinct, could be substituted as suggested by Atkinson (1988) and Simberloff (1990). Such experiments would provide valuable insights for reactivating pre-human patterns of resource use by birds but would always be somewhat contrived. The substitution of species lost from a particular system with closely related species, or extant subspecies from other regions, may be of wider application (Atkinson 1988). If for example, Brown Kiwi, Little Spotted Kiwi and New Zealand Snipe were established on a suitable island, three-quarters of the original group of subsurface insectivores would be restored. A population of Rock Wrens *Xenicus gilviventris* might be established on a suitable island and thus restore *Xenicus* genotypes to lowland habitats and selection pressures (Atkinson 1989). Such proposals rest heavily on islands at present but options for mainland management are slowly widening, as for example the management of Kokako at Mapara in the North Island (Saunders 1990).

What point is there in trying to turn back the clock in this way? Overcoming the practical and theoretical difficulties of such restoration challenges will teach us so much more about the birds we are trying to protect, their interactions with other animals and with plants, and the key ecological processes controlling their numbers, that it will enhance their chances of survival into the future.

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APPENDIX 1 – WEIGHTS OF NEW ZEALAND FOREST BIRDS

Weights of bird species referred to in this paper are listed below in order of the Checklist (Turbott 1990) together with sources of data. Weights estimated by P.R. Millener (unpub.) are based on allometric relationships between femur dimensions and body weight.

* = species that became extinct during Polynesian period; ** = species that became extinct during European period.

Species	Sex	n	Weight (kg)		Source of information
			Mean	Range	
<i>Anomalopteryx didiformis</i> *		16	41.3	31.7- 58.7	Atkinson and Greenwood (1989); North and South I. sample.
<i>Pachyornis elephantopus</i> *		20	146.0	96.7-247.4	Atkinson and Greenwood (1989).
<i>P. mappini</i> *		-	30.0	-	Anderson (1989).
<i>Emeus crassus</i> *		24	74.9	45.6-120.1	Atkinson and Greenwood (1989).
<i>Euryapteryx geranoides</i> *		19	95.7	48.7-139.9	Atkinson and Greenwood (1989); South I. sample.
<i>E. curtus</i> *		-	22.0	-	Anderson (1989).
<i>Dinornis struthoides</i> *		12	96.2	82.0-114.8	Atkinson and Greenwood (1989); South Island sample recorded as <i>D. torosus</i> .
<i>D. novaezealandiae</i> *		8	143.7	100.0-199.7	Atkinson and Greenwood (1989); South Island sample.
<i>D. giganteus</i> *		10	177.9	133.6-272.7	Atkinson and Greenwood (1989); South Island sample.
<i>Aptervx australis mantelli</i>	M	15	2.1	1.75-2.75	Colbourne and Kleinpaste (1983).
	F	31	2.5	2.0-4.0	
<i>Apteryx owenii</i>	M	10	1.2	1.04-1.29	R. Colbourne (pers. comm.).
	F	10	1.3	1.09-1.49	
<i>Hymenolaimus malacorhynchos</i>	M	-	0.90	-	M.J. Williams (pers. comm.).
	F	-	0.765	-	
<i>Anas aucklandica chlorotis</i>	M	-	0.630	-	M.J. Williams (pers. comm.).
	F	-	0.590	-	
<i>Euryanas finschi</i> *		-	-	c.2.2-2.3	P.R. Millener (unpub.).

Species	Sex	n	Weight (kg)		Source of information
			Mean	Range	
<i>Circus approximans</i>	M	42	0.649	0.542-0.726	Redhead(1969).
	F	29	0.839	0.744-1.044	
<i>C. eylesi</i> *	F	-	-	c.2.5-3.0	Holdaway (1989)
<i>Harpagornis moorei</i> *	M	-	-	c.9.0-10.0	Holdaway (1989).
	F	-	-	c.12.0-13.0	
<i>Falco novaeseelandiae</i>	M	5	0.265	0.245-0.280	National Museum (1990)
	F	3	0.466	0.415-0.510	
<i>Rallus dieffenbachii</i> * (see Table 12)		-	c.0.370	0.340-0.400	P.R. Millener (unpub.).
<i>R. modestus</i> *		-	c.0.066	c.0.050-0.070	P.R. Millener (unpub.).
<i>Gallirallus australis</i>	M	-	-	0.900-1.000	A.J. Beauchamp (pers. comm.); Kapiti Island sample
	F	-	-	0.650-0.750	
<i>G. a. scotti</i>	M	33	0.910	0.570-1.125	A. Roberts (pers. comm.).
	F	24	0.689	0.505-0.835	
<i>Capellirallus karamu</i> *		-	-	c.0.250-0.300	Holdaway (1989).
<i>Diaphorapteryx hawkinsi</i> *		-	c.2.00	c.1.80-2.30	P.R. Millener (unpub.).
<i>Gallinula hodgeni</i> *		-	-	c.0.400-0.500	Holdaway (1989).
<i>Porphyrio mantelli hochstetteri</i>	M	99	2.93	2.59-3.40	J.A. Mills (pers. comm.).
	F	81	2.46	2.24-2.80	
<i>Fulica chathamensis</i> *		-	-	c.1.2-1.4	P.R. Millener(unpub.).
<i>Aptornis otidiformis</i> *		-	-	c.10.00-11.0	Holdaway (1989, pers. comm.).
<i>A. defossor</i> *		-	-	c.12.0-13.0	Holdaway (1989, pers. comm.).
<i>Coenocorypha pusilla</i>		8	0.088	0.080-0.096	D.V. Merton (pers. comm.).
<i>C. chathamica</i> *		-	c.0.105	-	Authors' estimate based on size relative to <i>C. Pusilla</i> .
<i>Catharacta skua lonnbergi</i>	M	7	1.700	1.470-1.875	National Museum (1990).
	F	3	1.800	1.728-1.895	
<i>Hemiphaga n. novaeseelandiae</i>		-	0.650	-	Clout et al. (1991).
<i>H. n. chathamensis</i>		-	-	0.680-0.960	D.V. Merton (pers. comm.).
<i>Strigops habroptilus</i>	M	39	2.06	1.50-3.00	Merton et al. (1984).
	F	18	1.28	0.95-1.64	
<i>Nestor meridionalis septentrionalis</i>	M	10	0.506	0.460-0.560	R. Moorhouse (pers. comm.); Kapiti I. sample.
	F	5	0.416	0.390-0.440	

Species	Sex	n	Weight (kg)		Source of information
			Mean	Range	
<i>N. m. meridionalis</i>	M	16	0.595	-	P.R. Wilson (pers. comm.).
	F	16	0.500	-	
<i>Cyanoramphus n. novaezealandiae</i>	M	-	0.085	-	R. Powlesland (pers. comm.).
	F	-	0.065		
<i>C. n. chathamensis</i>	M	13	0.089	0.062-0.101	R.H. Taylor (pers. comm.).
	F	7	0.074	0.060-0.089	
<i>C. auriceps auriceps</i>	M	9	0.049	0.045-0.052	C.F.J. O'Donnell, P.J. Dilks, G.P. Elliott (pers. comm.).
	F	4	0.039	0.034-0.042	
<i>C. forbesi</i>	M	2	0.086	0.079-0.092	R.H. Taylor(pers. comm.).
	F	1	0.065	-	
<i>Chrysococcyx lucidus</i>		19	0.025	0.022-0.028	Robertson et al. (1983).
<i>Eudynamys taitensis</i>		4	0.126	0.111-0.140	Robertson et al. (1983).
<i>Ninox novaeseelandiae</i>		60	0.174	0.140-0.216	Robertson et al. (1983).
<i>Sceloglaux albifacies</i> *		-	c.0.500	-	P.R. Millener (unpub.).
<i>Megaegotheles novaezealandiae</i> *		-	c.0.200	-	Holdaway (1989).
<i>Halcyon sancta</i>		45	0.064	0.055-0.075	Robertson et al. (1983).
<i>Acanthisitta chloris granti</i>	M	21	0.006	0.005-0.007	Robertson et al. (1983)
	F	6	0.008	0.007-0.008	
<i>Xenicus longipes</i>		-	0.015	-	P.R. Millener (unpub.).
<i>Traversia lyalli</i> **		-	0.022	-	P.R. Millener (unpub.).
<i>Pachyplichas yaldwyni</i> *		-	0.050	-	P.R. Millener (unpub.).
<i>P. jagmi</i> *		-	0.040	-	P.R. Millener (unpub.).
<i>Bowdleria punctata</i>	M	25	0.036	0.033-0.040	Best(1973).
	F	17	0.034	0.028-0.037	
<i>B. rufescens</i> **		-	c.0.039	-	Authors' estimate, based on bone sizes relative to those of <i>B. punctata</i>
<i>Mohoua albicilla</i>	M	24	0.019	0.016-0.021	Robertson et al. (1983).
	F	15	0.015	0.012-0.020	
<i>M. novaeseelandiae</i>	M	51	0.013	0.012-0.015	J.B. Cunningham (1984).
	F	24	0.011	0.010-0.012	
<i>Gerygone igata</i>		112	0.006	0.005-0.008	Robertson et al. (1983).

Species	Sex	n	Weight (kg)		Source of information
			Mean	Range	
<i>G. albofrontata</i>	M	39	0.011	0.010-0.014	Robertson and Dennison (1984).
	F	11	0.010	0.008-0.012	
<i>Rhipidura fuliginosa placabilis</i>		92	0.008	0.006-0.010	Robertson et al. (1983).
<i>Petroica macrocephala toitoi</i>	M	51	0.011	0.009-0.014	Robertson et al. (1983).
	F	33	0.011	0.009-0.013	
<i>P. m. chathamensis</i>		-	-	0.014-0.018	D.V. Merton (pers. comm.).
<i>Petroica australis</i>	M	46	0.037	-	J.R. Hay (pers. comm.).
	F	19	0.035	-	
<i>P. traversi</i>	M	-	-	0.023-0.025	D.V. Merton (pers. comm.).
	F	-	-	0.020-0.022	
<i>Notiomystis cincta</i>	M	64	0.038	-	Rasch (1985).
	F	47	0.030	-	
<i>Anthornis m. melanura</i>	M	202	0.031	0.021-0.038	Robertson et al. (1983).
	F	94	0.024	0.020-0.032	
<i>A. m. melanocephala</i> **		-	c.0.038	-	Authors' estimate based on bone sizes relative to those of <i>A. m. melanura</i> .
<i>Prothemadera n. novaeseelandiae</i>	M	75	0.125	0.097-0.150	Robertson et al. (1983).
	F	46	0.090	0.070-0.105	
<i>Callaeas cinerea wilsoni</i>		61	0.229	0.195-0.265	J. Innes, C.R. Veitch and J.R. Hay (pers. comm.); Central North Island sample.
<i>Philesturnus carunculatus rufusater</i>	M	138	0.081	0.068-0.092	P.F. Jenkins and C.R. Veitch (pers. comm.).
	F	83	0.069	0.062-0.080	
<i>P. c. carunculatus</i>	M	11	0.085	0.082-0.091	A. Roberts (pers. comm.).
	F	14	0.072	0.067-0.077	
<i>Heteralocha acutirostris</i> **		-	c.0.295	-	P.R. Millener (unpub.).
<i>Turnagra capensis</i> **		-	c.0.100	-	Authors' estimate based on body size relative to <i>Turdus merula</i> .
<i>Palaeocorax moriorum</i> *		-	-	0.900-1.00	Holdaway (1989).

PLENARY LECTURE

**RECENT AVIFAUNAL CHANGES AND
THE HISTORY OF ORNITHOLOGY
IN NEW ZEALAND**

Ben D. Bell

RECENT AVIFAUNAL CHANGES AND THE HISTORY OF ORNITHOLOGY IN NEW ZEALAND

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ABSTRACT. New Zealand was one of the last land areas to be colonised by humans. During its long period of geographic isolation and in the absence of land mammals (except two genera of bats) an impressive endemic avifauna developed, much of which was vulnerable to ecological changes brought about by human settlement. During the Polynesian phase, beginning about 1000 years BP, many distinctive and often flightless endemics became extinct, including all the moas, while during European settlement (over the past 200 years), more bird extinctions and declines occurred. Major factors in these declines were habitat modification, hunting and the impact of introduced predators, particularly rodents and carnivores. Other birds have recently naturalised as a result of deliberate introductions (mostly from Europe) or self-colonisation (from Australia). Ornithological research in New Zealand began with the voyages of Captain Cook, followed by pioneering studies in the nineteenth century, when specimens were avidly collected for museums and private collections. Later in the nineteenth century increasing conservation awareness developed, leading to the conservation-oriented research and management which dominates New Zealand ornithology today.

Keywords: Bird conservation, endemism, extinction, human impact, New Zealand, predation.

INTRODUCTION

Atkinson & Millener (1991) describe the pre-human avifauna of New Zealand and speculate on the community relationships of particular habitats. The present paper focuses on ornithological events following human settlement and outlines the history of ornithological study in New Zealand. The new *Checklist of the birds of New Zealand* (Turbott et al. 1990) is used as the basis for taxonomy and nomenclature in this contemporary summary and interpretation of the New Zealand avifauna. Scientific names of New Zealand birds are generally not included in the text, but can be found in the *Checklist*. The only additional species is an undescribed subfossil NZ wren (Passeriformes; Acanthisittidae) noted by Millener (1988). For this paper the New Zealand region extends from the subtropical Kermadec Islands in the north to the subantarctic islands in the south (including Macquarie Island, as shown on page 246 in the 1990 *Checklist*), but excluding the NZ Ross Dependency in Antarctica.

COMPOSITION OF THE NEW ZEALAND AVIFAUNA

Ornithologically New Zealand is recognised for its distinctive endemic land birds and for its diversity of seabirds. However, the total recorded avifauna comprises many other species too. Within the region defined above, 380 species have been recognised from 198 genera, 64 families and 20 orders (Table 1, Figure 1). Half of the species breed in New Zealand though 47 arrived since 1800. A third of the species are non-breeders, mostly irregular or uncommon visitors such as Australian vagrants, northern waders and oceanic seabirds. Fossil, subfossil and extinct species comprise 16% of species in the *Checklist* (Table 1).

TABLE 1 - Summary of New Zealand avifauna. Based on *The Checklist of the birds of New Zealand* (Turbott et al. 1990) but excluding the Ross Dependency region of Antarctica and including an additional *Acanthisittid* reported by Millener (1988).

62 Fossil/extinct species (16.3%)
17 Fossils
35 Subfossils
9 Extinct since 1800
1 Subfossil, still extant overseas
 193 Breeding species (50.8%)
9 Self-colonised since 1800
38 Exotic introductions since 1800
146 Other breeding species
 125 Non-breeding species (32.9%)
110 Irregular/uncommon visitors
15 Regular visitors
 Total: 380 Species

The New Zealand avifauna is dominated by three orders - the Procellariiformes (65 species), the Charadriiformes (85 species) and the Passeriformes (53 species). The Charadriiformes comprise 59 waders, 5 skuas, 3 gulls and 18 terns. Many of them are visiting non-breeders, including trans-equatorial migrant palaeartic waders like the Lesser Knot and the Bar-tailed Godwit. The 65 Procellariiformes dominate the 134 marine species. Given this diversity, New Zealand has appropriately been described as the “seabird capital of the world”. Apart from a wide range of petrels (Procellariiformes), there are 27 species of penguins (order Sphenisciformes, 14 of which are fossils), 25 Pelecaniform species (dominated by 13 shag species) and various Charadriiformes. The seabirds form three major geographical groups: subtropical species from warmer waters of northern New Zealand and the Kermadecs; temperate species from the main islands around and south of New Zealand; and circumpolar species from the rich, cool seas of the Antarctic and subantarctic. The 53 species of Passeriformes now dominate the land birds. Most are local breeders, though 16 are exotics deliberately brought to New Zealand during European settlement.

While 17 fossil and 36 subfossil species from 40 genera have been described from New Zealand (Table 1), the avian fossil record from before the Late Pleistocene is very sparse (Millener 1990), only a few orders being represented (Procellariiformes, Sphenisciformes, Pelecaniformes, Anseriformes). Most are from consolidated, generally marine Early Pleistocene deposits. Many more taxa (36 species and 27 genera) are described from the last glacial and younger (subfossil) deposits, their unconsolidated remains coming from dune sands, cave silts, buried soils and fluvial or swamp deposits (Millener 1990). Further species have yet to be described, including the *Acanthisittid* wren included in this analysis (a curve-billed species described as the “tree-creeping wren” - P.R. Millener, pers. comm.). Recent extinctions (over the past 1000 years) include terrestrial and wetland species, but not seabirds.

FEATURES OF THE NEW ZEALAND AVIFAUNA

To better understand the impact of human settlement on New Zealand birds, some of their features will first be briefly outlined. Fuller accounts of the pre-human avifauna of New Zealand include Atkinson & Millener (1991), Holdaway (1989) and Millener (1990). Trends evident in New Zealand birds include a high degree of endemism, K-selected endemics, a high proportion of flightless taxa, melanistic and polymorphic plumages, tameness and vulnerability (to mammalian predators), and evidence of successive colonisations of related species.

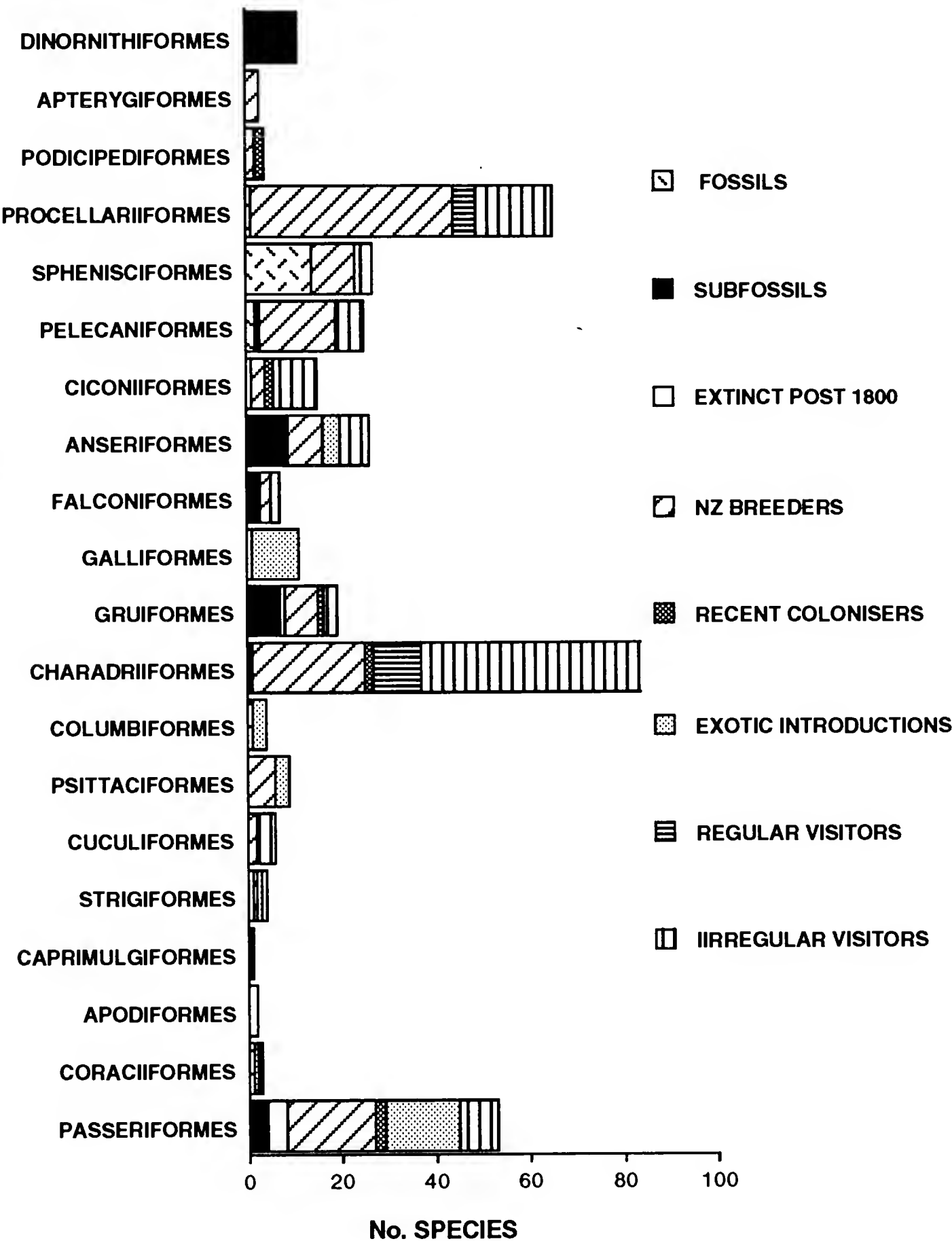
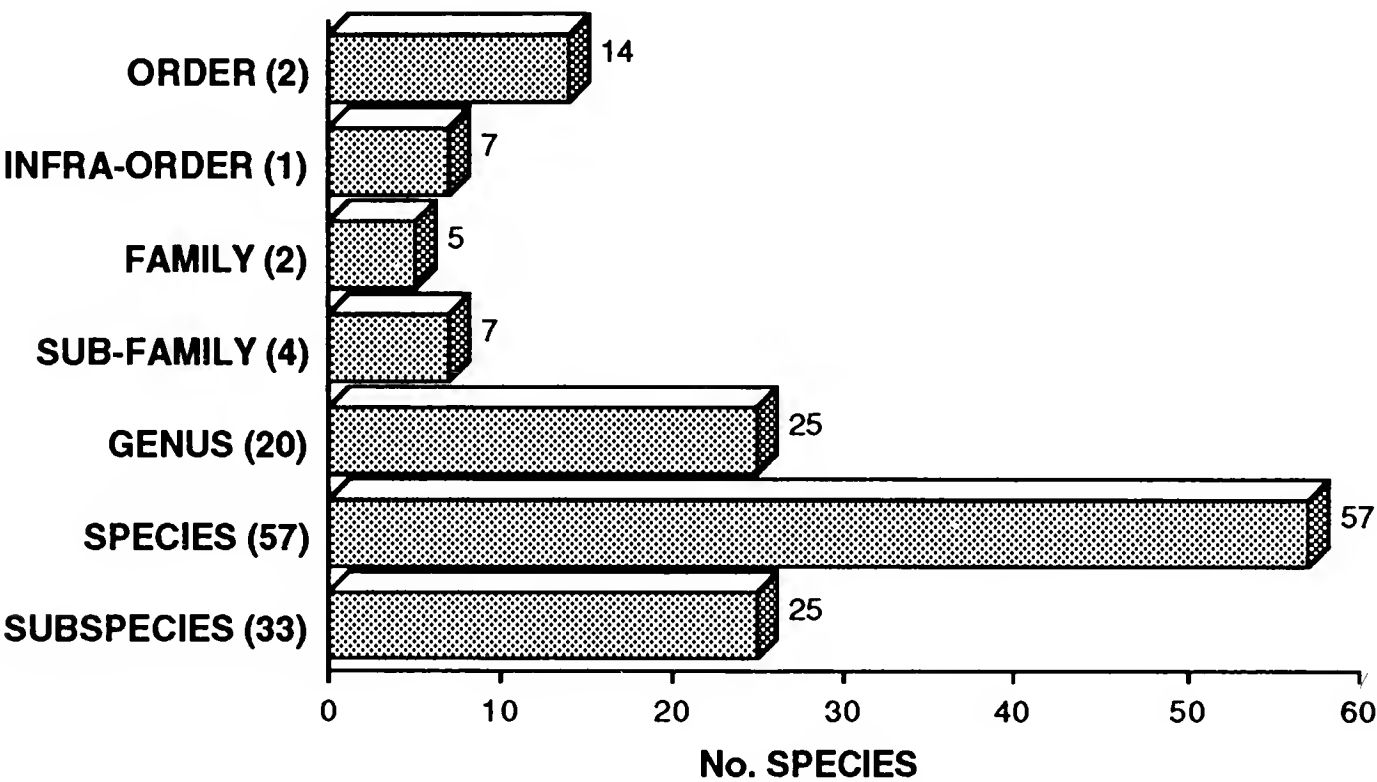


FIGURE 1 - The major groups of bird species recorded in the New Zealand region classified by order and the categories summarised in Table 1.

High degree of endemism

A high level of endemism is a feature of New Zealand’s avifauna: 115 species are endemic at the species level, or higher, while a further 25 species are represented by endemic subspecies in New Zealand (Table 2, Figure 2). Excluding the 17 fossil species (Table 1), 223 non-endemic species make up the rest of the New Zealand list (Table 2). In drawing up this Table 2, NZ Pigeon, Red-crowned Parakeet and the parrot genus *Nestor* are regarded as New Zealand endemics, although their recorded distribution also extends to either Lord Howe Island or Norfolk Island (Turbott et al. 1990). Totally endemic orders comprise the Dinornithiformes (11 extinct moas) and the Apterygiformes (3 extant kiwis). DNA sequence data used to create a phylogeny for the ratites - including the extinct moas - indicate that the two New Zealand orders are not monophyletic (G. Chambers & A. Cooper, pers. comm.). Endemic at the Infra-order level are the suboscine Acanthisittidae - the highly distinctive NZ wrens - comprising 2 extant species (Rifleman, Rock Wren) and 5 extinct species (Bush Wren, Stephens Island Wren, 2 Stout-legged Wrens and an undescribed species (Millener 1988).

FIGURE 2 - Levels of endemism in New Zealand birds.



There are two endemic families - the Gruiform Aptornithidae (2 *Aptornis* species) and the Passeriform Callaeidae (Kokako, Saddleback and Huia). The four endemic sub-families comprise the Strigopinae (Kakapo), the Nestorinae (Kaka and Kea), the Mohouinae (Whitehead, Yellowhead and Brown Creeper) and the Turnagrinae (Piopio). Many more New Zealand birds are endemic at lower taxonomic levels (Table 2, Figure 2): 25 species are endemic at the generic level (20 genera involved), while 57 are endemic at the species level. The additional 25 species with endemic New Zealand subspecies embrace a total of 33 local subspecies. New Zealand subspecies of more widely distributed species include the South Island Pied Oystercatcher, Morepork, Shining Cuckoo, North, South and Chatham Island Fantails and New Zealand, Chatham, Auckland and Antipodes Island Pipits. Others are more local, such as two rails - the Marsh Crake *Porzana pusilla affinis*, and the Auckland Island Rail *Rallus pectoralis muelleri*, the latter rediscovered only last summer (Elliott 1990b). Three subspecies of the Banded Rail are known from the New Zealand region - *Rallus philippensis assimilis* from the main islands, *macquariensis* from Macquarie Island (extinct) and *dieffenbachii* from the Chatham Islands (extinct).

TABLE 2 - Levels of endemism in different orders of New Zealand birds (excluding fossils).

No. species endemic at different taxonomic levels									
	Order	Infra order	Family	Sub family	Genus	Species	Sub species	Other species	Total species on N.Z. list
Dinornithiformes	11	-	-	-	-	-	-	0	11
Apterygiformes	3	-	-	-	-	-	-	0	3
Podicipediformes	-	-	-	-	-	1	-	3	4
Procelariiformes	-	-	-	-	-	13	7	44	64
Sphenisciformes	-	-	-	-	1	3	1	8	13
Pelecaniformes	-	-	-	-	2	7	3	11	23
Ciconiiformes	-	-	-	-	-	1	-	14	15
Anseriformes	-	-	-	-	5	7	2	12	26
Falconiformes	-	-	-	-	1	3	-	3	7
Galliformes	-	-	-	-	-	-	1	10	11
Gruiformes	-	-	2	-	3	5	3	6	19
Charadriiformes	-	-	-	-	5	7	4	69	85
Columbiformes	-	-	-	-	1	-	-	3	4
Psittaciformes	-	-	-	3	-	3	0	3	9
Cuculiformes	-	-	-	-	-	1	-	5	6
Strigiformes	-	-	-	-	1	-	1	2	4
Caprimulgiformes	-	-	-	-	1	-	-	0	1
Apodiformes	-	-	-	-	-	-	-	2	2
Coraciiformes	-	-	-	-	-	-	1	2	3
Passeriformes	-	7	3	4	5	6	2	26	53
TOTALS	14	7	5	7	25	57	25	223	363

K-selected endemics

Many specialised endemic birds of New Zealand are typical K-selected species (Pianka 1974). The resulting specialist life-style has rendered them more vulnerable to extinction in the changing environment following human settlement. K-selected species are characteristically large, relatively sedentary and long-lived, with low annual productivity and delayed maturity (Pianka 1974). An evolutionary transition from an r-selected coloniser to a K-selected endemic can be invoked when comparing some older endemics with closely related species that have arrived in New Zealand more recently - e.g. the Takahe representing the K-selected endemic and the congeneric Pukeko the r-selected coloniser (Table 3).

High proportion of flightless taxa

Associated with the K-selected trend for increased size is a tendency towards loss of flight. Over half of the endemic land bird avifauna (i.e. excluding seabirds) are flightless, have weak flight, or are reluctant fliers. Flightlessness is a feature of oceanic island avifaunas, and is generally associated with a lack of mammalian predators, allowing the birds to be 'released' from the physical and energetic demands of powered flight. On small predator-free islands the reduced need for dispersal is particularly evident; indeed, where winds are especially strong flying may carry risks of drifting out to sea. Generally the reduction in wing size is associated with reduced pectoral musculature and a smaller carina on the sternum, while New Zealand flightless

TABLE 3 - Life history traits in the Takahe and the Pukeko.

	Takahe K-selected	Pukeko r-selected
Weight (kg)	2.2-3.2	0.8-1.4
Length (mm)	630	510
Flighted	No	Yes
Status	Endemic	Native
Rarity	Endangered	Abundant
Distribution	Very local	Widespread
Breeding	Oct-Feb	Aug-Feb+
Clutch size	2	5-6
Incubation (DAYS)	30	24
Broods/year	1	2-3
First breed (Years)	3	1 +

TABLE 4 - Flightless New Zealand birds (excluding 14 fossil and 13 modern pen- guins).

Order	Taxa	Status
Dinornithiforms	11 Moas	extinct
Apterygiformes	3 Kiwis	declined
Anseriformes	<i>Cnemiornis calcitrans</i>	extinct
	<i>Cnemiornis gracilis</i>	extinct
	Auckland Is. Teal	declined
	Campbell Is. Teal	declined
	<i>Pachyanas chathamica</i>	extinct
	<i>Euryanas finschi</i>	extinct
	(?) Auckland Island Merganser	extinct
Gruiformes	Weka	declined
	NZ Snipe-rail	extinct
	Giant Chatham Is. Rail	extinct
	Hodgen's Rail	extinct
	Takahe	declined
	Chatham Is. Coot	extinct
	NZ Coot	extinct
	North Is. <i>Aptornis</i>	extinct
	South Is. <i>Aptornis</i>	extinct
Psittaciformes	Kakapo	declined
Passeriformes	Stephens Is. Wren	extinct
	(?) South Is. Stout-legged Wren	extinct
	(?) North Is. Stout-legged Wren	extinct
	Tree-creeping Wren	extinct
Totals	32+ Taxa	24+ Extinct

forms tend to increase the width and/or length of the legs. The energy conservation advantage of flightlessness is recognised (Fleming 1982, McNab 1990), though some flightless species have retained pectoral wing musculature and adopted an

alternative power-use for the wings, e.g. penguins. Amongst the New Zealand avifauna all 11 extinct moas and all 3 extant kiwis are entirely flightless.

Flightlessness, often associated with large size, is more prevalent in New Zealand birds than elsewhere and includes three entire orders: two ratite orders (moas and kiwis) and the penguins. At least 18 further taxa are totally flightless (Table 4), while at least 15 others have rather weak flight or are reluctant fliers (Brown Teal, Auckland Island Merganser (? flightless), Chatham Island Rail, NZ Snipe, Chatham Island Snipe, NZ Owlet-nightjar, Bush Wren, Rock Wren, Fernbird, Chatham Island Fernbird, Kokako, Saddleback, Huia, 2 Stout-legged Wrens (?flightless) (Williams (1973), Fleming (1982), Holdaway (1989), P.R. Millener (pers. comm.)).

In New Zealand, as elsewhere, the Rallidae show a strong tendency towards flightlessness. Even many volant forms (e.g. *Rallus. Porzana*) are typically reluctant fliers, though they may nevertheless be capable of flying long distances. Totally flightless rallids include the extant Weka (4 subspecies) and Takahe (2 subspecies), and the extinct Snipe-rail, Giant Chatham Island Rail, Hodgen's Rail, Chatham Island Coot and NZ Coot. As with the two *Porphyrio* species (Takahe and Pukeko, Table 2), the flightless and flighted NZ Coots (*Fulica* spp.) probably represent successive invasions of New Zealand; the flighted Australian Coot is still expanding at present (Turbott et al. 1990). While Olson (1973a) invoked recent flighted dispersal prior to flightlessness in insular Rallidae, Beauchamp (1989) takes an alternative view for New Zealand *Gallirallus* (classification following Olson 1973b), arguing for a more ancient origin on the basis of panbiogeographic analysis. Also in the order Gruiformes were two flightless species of *Aptornis* (or Adzebill), distinctively large flightless birds with a unique jaw mechanism and a suggestive resemblance to the Rhynchotidae (Kagu) of New Caledonia (Turbott et al. 1990).

Within the Anatidae, the endemic NZ Brown Teal species complex provides an interesting example of variations in flight capability. The New Zealand mainland subspecies *A. aucklandica chlorotis* is a more reluctant flier than the closely-related Chestnut Teal *Anas castanea* of Australia. The 'strong' subantarctic subspecies of Brown Teal on the Auckland Islands (*aucklandica*) and on Dent Island off Campbell Island (*nesiotis*, formerly thought extinct) are both flightless and more K-selected than *chlorotis*. Recent electrophoretic studies indicate these two island subspecies have independently lost their power of flight (C.H. Daugherty, pers. comm.). A further undescribed subfossil form of Brown Teal which occurred in the Chatham Islands also exhibited wing reduction, though it was probably a weak flier (P.R. Millener, pers. comm.). Worthy (1988) has compared subfossil *Euryanas* from different aged deposits and detected a 10 percent reduction of wing-size between the later Otiran glacial-early Holocene (20000-11000 years BP) and the late Holocene (2000-1000 years BP). The more recent subfossils had become about as flightless as the extant Auckland Island Teal; Millener (pers. comm.) regards both populations of *Euryanas* as flightless.

Melanism and polymorphism

New Zealand birds show a relatively high incidence of melanism which Fleming (1982) suggests is a result of a "release from selection pressures such as predation [which] seemingly allowed some species to abandon the patterns of countershading that had proved advantageous in most parts of the world". Melanic or darkened plumages occur in the rails, in two species of normally white-breasted shags, in oystercatchers, stilts, fantails, tits, and robins. Some melanic forms are full species (e.g. Black Stilt

and Black Robin), others are geographic subspecies (e.g. Snares Island Tomtit *P. macrocephala dannefaerdi*), or are morphs in dimorphic or polymorphic populations (e.g. black and pied morphs of the Fantail).

Tameness and vulnerability

The notion that New Zealand was “predator-free” prior to the arrival of humans and associated predatory mammals is incorrect. Holdaway (1989), Millener (1990) and Atkinson & Millener (1991) provide insights into the pre-human avian communities of New Zealand, communities in which both diurnal and nocturnal avian predators existed, including two raptors - the *Harpagornis* eagle and a goshawk (in the *Checklist* as *Circus eylesi*) - which were the largest of their kind anywhere in the world. There were also non-avian predators on the mainland e.g. the Tuatara *Sphenodon punctatus* (Reptilia; Sphenodontidae), still a petrel predator on offshore islands. Despite such predators, the endemic avifauna evolved in New Zealand in the absence of humans and diurnal or nocturnal mammalian predators and competitors. Many species - and particularly more specialised endemics - were therefore ill-equipped for survival once such mammals arrived (Holdaway 1989). Such vulnerability manifested itself in a variety of ways: for instance, by tameness to a degree that offered little resistance to predation (including by humans); by choice of nest sites, roost sites or perch sites that were exposed to predators; or by having specialist diets depleted by more successful colonists.

Successive colonisations

Fleming (1962, 1974) identified a range of species pairs which he interpreted as representing possible double invasions of the same stock. Examples - with the earlier colonist first - are Weka and Banded Rail, NZ Coot and Australian Coot, Takāhe and Pukeko, Black Stilt and Pied Stilt, Robin and Tomtit.

GENERAL IMPACT OF HUMAN SETTLEMENT

New Zealand was one of the last land areas to be colonised by humans. Polynesians were the first human arrivals some 1000-1200 years ago. European settlement came much later, following the first voyage of Captain James Cook over 1768-71 (Kippis 1883). On a geological time scale human occupation has been very recent: if New Zealand's 70 million years of isolation were considered merely a day, then Polynesians arrived at roughly 1 second, and Europeans less than a quarter second, before midnight. Despite this late arrival the impact of human settlement on the biota and landscape has been considerable.

This human impact falls into three main categories:

- (i) habitat modification (by forest clearance, fire, agriculture and settlement);
- (ii) human hunting pressure (for food and other cultural reasons);
- (iii) introduction of exotic biota (deliberately or accidentally).

Habitat modification

While there have been modifications to all major bird habitats in New Zealand, the loss of forest habitat is the most striking change since human settlement. About 71% of the original forest has been lost since Polynesians arrived, the rate of loss markedly accelerating over the past 200 years since the European arrival.

POLYNESIAN PHASE. Untouched New Zealand was almost entirely covered with forest, at least below the treeline, representing about 78% of the land area (King 1984). During the Polynesian phase of settlement indigenous forest cover was reduced - mainly by fire - from 78% to 53% by 1840. The drier lowland podocarp forests of the eastern South Island were destroyed between 600 and 800 years ago, and the beech forests of the eastern inland mountain basins between 500 and 700 years ago. Forests were replaced by tussock grassland in these areas. Rapid deforestation was underway in the North Island by 600-800 years ago (King 1984).

EUROPEAN PHASE. During European pastoral development, forest cover declined from 53% of the land area in 1840 to about 23% at present (King 1984). The impact was particularly high in the biologically more diverse and species-rich lowland forests (< 2000 ft asl) which are very poorly represented nowadays. Application of European technology with a desire to 'tame the land' also resulted in considerable loss of other habitats, such as tussock grassland, wetlands and estuaries. Most of the present landscape (52%) is now open country, comprising pastoral grazing land, induced fern and tussock, or scrub (King 1984). Not only has the total area of forest been reduced to 23%, but remaining forests have become highly fragmented into scattered patches of varying size. Particularly fragmented are the lowland forests, and altitudinal sequences from low to high altitude forest have been lost in most parts of the country as fertile lowland areas have been converted to agriculture and other land uses.

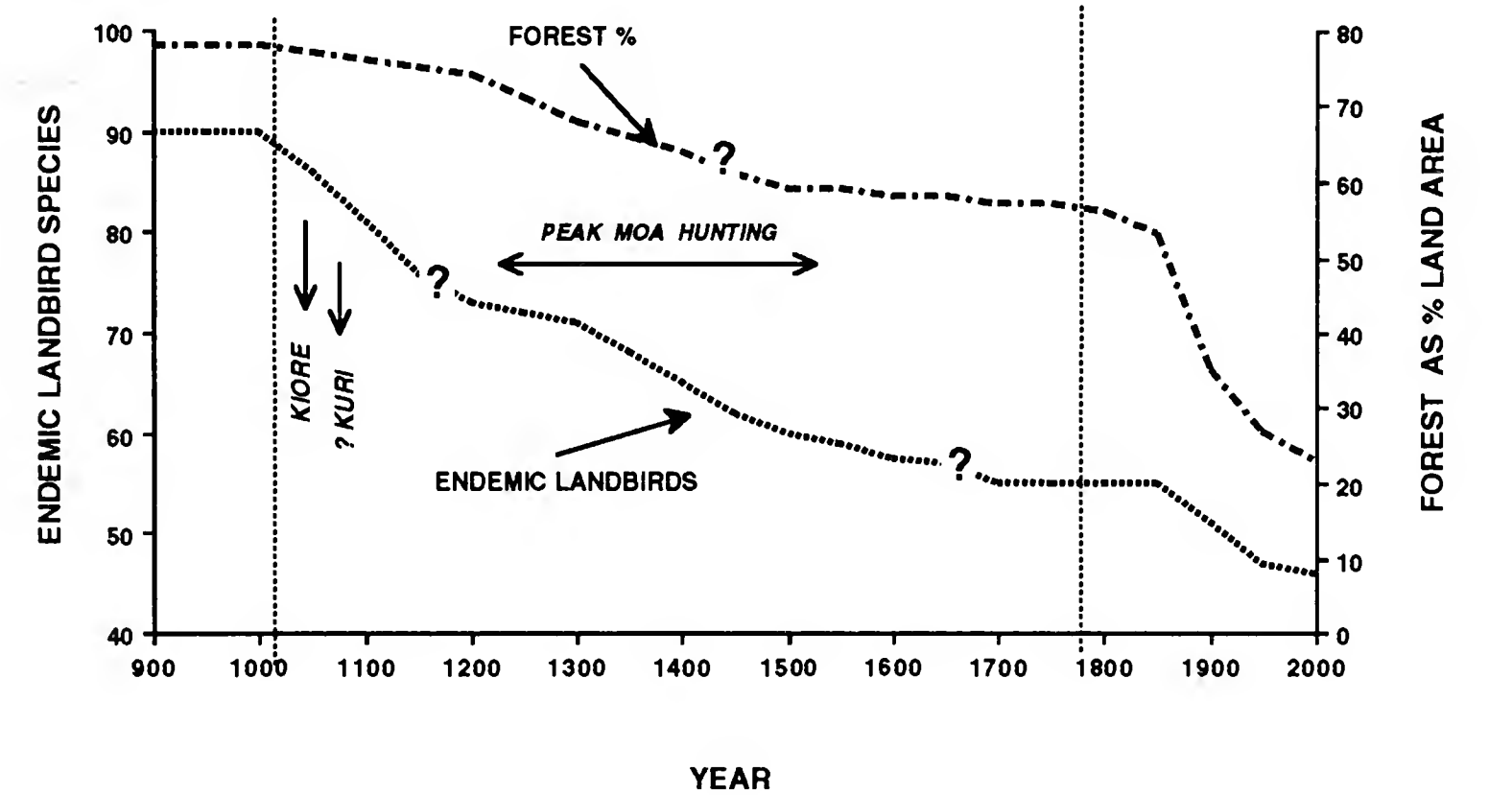


FIGURE 3 - Diagrammatic summary of the decline in native forest and endemic bird species in New Zealand since human settlement. Precise data are lacking, so this figure provides only an approximate scenario of the possible decline rates.

Hunting pressure

POLYNESIAN PHASE. There is widespread archaeological evidence that the Polynesian settlers exploited native birds for food (King 1984, Holdaway 1989, McGlone 1989, Millener 1990). Remains of moas and a wide variety of other birds have been found in middens and other Polynesian sites (Millener 1990). McGlone (1989) has estimated the most intensive period of moa hunting was from about 800 to 550 years BP,

declining thereafter. Avian material became part of the culture in other ways also; for instance, the feathers of the now extinct Huia remain a symbol of high rank in Maori society.

EUROPEAN PHASE. During the European phase of settlement hunting was initially focussed on marine mammals - some of the earliest European settlers were sealers and whalers who plundered these animals around the New Zealand coast (King 1984). However, during the course of the nineteenth century hunting increased on often dwindling stocks of native birds. These native birds were taken for food, adornment, science or just recreation. The introduction of European weapons to both Maori and Pakeha cultures would have greatly increased the hunting efficiency.

Introduced biota

POLYNESIAN PHASE. Polynesians brought with them two other mammals - the kiore *Rattus exulans* (a Polynesian rat) and the kuri *Canis familiaris* (a domestic dog). The pig and the chicken, which accompanied Polynesian settlement elsewhere in the Pacific, apparently failed to make the long journey to New Zealand (Prickett 1990). The kiore probably spread very rapidly through the mainland areas of New Zealand. The behaviour of the kuri after introduction is uncertain. Though the animal remained a commensal of Polynesian settlements until its disappearance last century, the extent to which it hunted beyond these settlements has been a matter of speculation (King 1984, Holdaway 1989, Anderson 1990).

EUROPEAN PHASE. A much greater range of exotic biota was brought to New Zealand during the European phase of settlement (King 1984). Indeed the pressure for introducing more species continues today. The terrestrial vertebrates known to have naturalised in New Zealand comprise 3 amphibians (all frogs), 1 reptile (a skink); 39 birds and 33 mammals (McDowall 1969, Bell et al. 1985, Turbott et al. 1990, King 1984).

Impact of human settlement on avifauna

The loss of the Dodo on Mauritius, the Great Auk in the North Atlantic, and the Passenger Pigeon in North America, all evoke strong emotions about bird extinction. Indeed these bird species have become symbols of extinction events in general. But in New Zealand - in an ancient and unique assemblage so distinctive that Diamond (1990) chose to call the region the world's smallest continent - we have lost not one or two, but dozens of bird species, amounting to an ornithological and ecological change of dramatic proportions. That human-accelerated process of extinction still continues, despite the dedicated effort of New Zealand bird conservation.

AVIFAUNAL CHANGES

As a result of human settlement some species have gained by colonising or expanding their former ranges in New Zealand. However, on balance gains fall well short of the losses:

Gains 53+ species	
Increase in range and numbers	9 species
Colonisation by new species	44+ species
Losses 104+ species	
Reduction in range and numbers	59+ species
Totally extinct	44 species
Extinct NZ, surviving overseas	1 species

Moreover, those that have benefited are generally common, non-endemic birds colonising from adjacent areas (especially Australia) or are abundant species deliberately introduced by Europeans. An indication of land bird declines over the last 1000 years is given in Figure 3.

Increases in range and numbers

Gains occurred in three main groups of birds:

- (i) Native species whose range and numbers increased naturally, mainly as a result of human-induced environmental changes.
- (ii) Species naturally colonising New Zealand since human settlement.
- (iii) Exotic species deliberately introduced by human settlers.

Increases of native species

Relatively few native bird species have increased in range and numbers following human settlement, most as a result of habitat changes since 1800 (e.g. more open habitat or increased food supplies). They include the Westland Petrel, Australasian Gannet, Little Black Shag, Paradise Shelduck, Black-backed Gull, Black-billed Gull, Australasian Harrier and NZ Pipit. Some increases (e.g. the Westland Petrel and Australasian Gannet) may represent only recent recovery after earlier human exploitation.

Self-colonisers

While many native bird species presumably first reached New Zealand by trans-oceanic dispersal, especially from Australia (Falla 1953, Fleming 1962, McDowell 1969), some can be identified as recent settlers. Species introduced during the European phase of settlement have also subsequently colonised new areas, such as the Chatham Islands and subantarctic islands.

Species self-colonising prior to European settlement are the most difficult group to identify due to lack of documentation. They probably include two Australian species now widespread in New Zealand - Pied Stilt and Pukeko. Further Australian species have established since 1800, namely White-faced Heron, Royal Spoonbill, Australian Coot, Black-fronted Dotterel, Spur-winged Plover, Welcome Swallow, and Silvereye. Others have yet to establish breeding populations here (e.g. Cattle Egret), or are only limited breeders (e.g. Hoary-headed Grebe). At least one - the Little Black Shag - not represented in subfossil and midden material (Millener 1990) may also have established during the European phase. Successive waves of colonisation from Australia will have reinforced stocks of species like the White Heron (Kotuku), White-faced Heron, Little Black Shag and Royal Spoonbill, maintaining gene-flow. The White Heron was evidently present prior to Polynesian settlement (Millener 1990), as was the Grey Teal. Species like the Fantail, Grey Warbler, Robin and Tomtit have all speciated or subspeciated in New Zealand and probably represent earlier colonisations from Australia.

European introductions

All the birds successfully introduced by humans came during the European phase of settlement. Not all naturalised (Thomson 1922), including the Nene (Hawaiian Goose), European Robin, Nightingale, Linnet, Reed Bunting and Tree Sparrow. Those that did were successful colonists, generally common and widespread in their areas of origin. Prominent among these colonisers are European passerines, waterfowl and game

birds. Many are now widespread and have successfully colonised the forests of the mainland and some offshore islands, e.g. Kermadecs, Chathams and subantarctic. A few have remained, or become, more local. For instance the Common Myna is mostly confined to the northern half of the North Island, while the Cirl Bunting and some game birds are also relatively local in distribution (Bull et al. 1978). Initial stocks of the Australian Black Swan were deliberately introduced but have probably been supplemented by natural invasions of birds crossing the Tasman Sea (Williams 1985).

Declines in range and numbers

A consequence of human impact is that the country now has a disproportionately high number of the world's rare, vulnerable and endangered species. Moreover, New Zealand has proportionately more of its species in the 'endangered' category than the rest of the world (Figure 4) although other island groups, like Hawaii, also have high numbers of endangered bird taxa (King 1981).

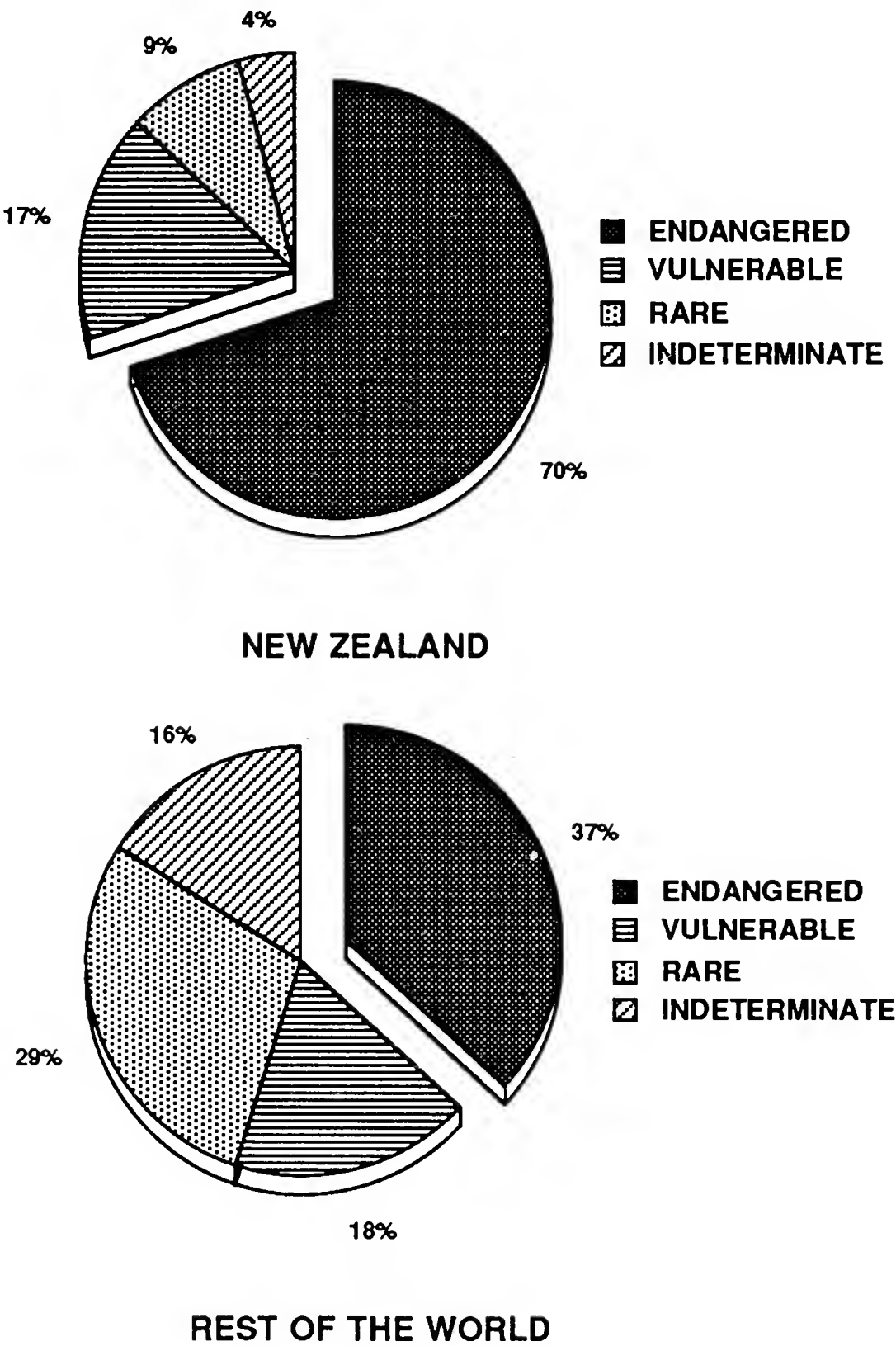


FIGURE 4 - ICBP Red Data Book categories for birds of New Zealand and the rest of the world. Based on most recent available world data listed by King (1981).

General declines

Many endemics still survive on the main islands, though their ranges and numbers are much reduced since pre-human times e.g. Brown Kiwi, Great Spotted Kiwi, Hutton's Shearwater, Sooty Shearwater, Diving Petrel, Yellow-eyed Penguin, Blue Penguin, NZ Dabchick, Australasian Crested Grebe, Reef Heron, Australasian Bittern, Grey Duck, Blue Duck, Brown Teal, NZ Scaup, NZ Falcon, Banded Rail, Weka, Takahe, Black Stilt, NZ Dotterel, NZ Fairy Tern, NZ Pigeon, Kaka, Red-crowned Parakeet, Yellow-crowned Parakeet, Morepork, Rifleman, Rock Wren, Fernbird, Whitehead, Yellowhead, Brown Creeper, NZ Tomtit, NZ Robin, Bellbird, Tui and Kokako.

Many species of seabirds declined on the mainland or became locally extinct as breeding colonies, now breeding only on offshore islands (e.g. Fairy Prion); Hutton's Shearwater and Westland Petrel continue to survive as mainland breeding colonies in the South Island. Other seabirds were known on the mainland in earlier European times (e.g. Black Petrel, Mottled Petrel). Remains of petrels are prominent in many cave deposits throughout New Zealand. When in forest areas, they probably reflect former breeding colonies. Dune deposits may also indicate former colonies rather than strandings (Millener 1981, Holdaway 1989).

Whether the Takahe was formerly widely distributed throughout North and South Island forest, or should be seen as a relict of the Pleistocene grassland avifauna, has been a matter of debate (Mills, Lavers & Lee 1984, 1988, Beauchamp & Worthy 1988). Whatever the extent of its range at the time of Polynesian settlement, the bird has evidently declined markedly in numbers, becoming extinct in the North Island and confined to a remnant population in the Murchison Mountains of the South Island (Mills et. al 1984, 1988). Indeed it was thought to be extinct until rediscovery by G.B. Orbell in 1948.

Markedly disjunct ranges

While fragmentation of former ranges has resulted in various species now having disjunct distributions, the ranges of some are now so markedly disjunct that they occupy widely separate breeding areas. The NZ Dotterel breeds around northern coasts of the North Island and on the uplands of Stewart Island, having disappeared from former breeding sites in the South Island high country in historical times (J. Dowding, pers. comm.). Cook's Petrel now breeds only in the Hauraki Gulf and on Codfish Island, off Stewart Island, yet is known from North Island cave, midden and swamp/alluvium/colluvium deposits and from South Island caves (Millener 1990).

Biological refugees

Since human settlement a number of species have become "biological refugees", confined to one or more "safe" offshore islands. They are termed "refugees" since they are no longer able to survive across their former natural range on the mainland or on parts of island groups, due primarily to the impact of mammalian predators. They are relictual species now confined to refuges on predator-free islands. Examples are Little Spotted Kiwi, Cook's Petrel, Chatham Petrel, Mottled Petrel, Chatham Island Taiko, Black Petrel, Campbell Island Teal, Auckland Island Teal, Shore Plover, NZ Snipe, Chatham Island Snipe, Kakapo, Forbes Parakeet, Black Robin, Stitchbird and Saddleback. Some of these refugee species are now limited to the smaller islands of island groups. For example Snipe, Yellow-crowned (Forbes) Parakeet and Black Robin on the Chatham Islands, the rail and Teal on the Auckland Islands and the

Campbell Island Teal - now one of the world's rarest birds (ca. 30 individuals) - on Dent Island. Refugee species remain vulnerable to future invasion of their habitats by predators. Several documented examples graphically bring home this risk. The Stephens Island Wren discovered in 1894 became almost immediately extinct when the domestic cat was introduced to Stephens Island (Falla, Sibson & Turbott 1979); ship rats *Rattus rattus* reached Big South Cape Island by 1962 and then exploded into a major irruption in 1964; the greater NZ short-tailed bat *Mystacina robusta* and probably the last extant population of Bush Wren (Stead's Bush Wren) went extinct, as did the local NZ Snipe subspecies.

Recovery of endemic rarities through conservation management

Over recent years the ranges and numbers of many "refugee" species have been extended by deliberate translocation to other island refuges and by other conservation management - for instance the Chatham Island Black Robin and Saddleback.

The Chatham Island Black Robin provides one of the most spectacular examples of a species' recovery, thanks to the efforts of the former NZ Wildlife Service, and now the Department of Conservation (Merton 1990). Following habitat destruction and the introduction of mammalian predators on the larger Chathams islands, a remnant Black Robin population of 20-30 birds persisted in 5-7 hectares of scrub on top of Little Mangere Island for about 90 years (Merton 1990). In the 1970s the woody vegetation there degenerated following the clearing of a helicopter pad (to allow access for mutton-birders) and the Black Robin population plummeted from 18 birds in 1973 to 7 birds (2 pairs, 3 males) in 1976. The Wildlife Service relocated the remaining birds on adjacent 130 ha Mangere Island, on which a revegetation programme was underway, in 1976 (Merton 1990). The population dropped to only five birds (2 females, 3 males) by September 1980, including only one effective breeding pair (female "Old Blue" and her mate "Old Yellow"). A negative exponential curve over this period of decline (1972-1976) predicts that, without further management, the species would have gone extinct by about 1982-83 (Figure 5). Despite being in such a dramatically critical situation, the Black Robin population has since recovered at an exponential rate (Figure 6), largely the result of an imaginative and innovative programme of intensive management by Don Merton and his colleagues. This involved further translocation to South East Island, predator and competitor control, improved nest security by provision of artificial nest sites and reconstruction of insecure nest sites, egg and brood transfers with cross-fostering initially to Chatham Island Warblers and then Chatham Island Tomtits, and continued habitat restoration (Merton 1990). Currently about 86 Black Robins (38 pairs) survive (D. Merton, pers. comm.). Intensive manipulative management ceased following the 1988/89 breeding season when 99 birds existed. Despite this, the population had increased by a further 17% to 116 birds a year later (February 1990), suggesting the population was in a position to continue recovery without further brood manipulation. The carrying capacity of the available habitat has yet to be reached: while the latest November figure (86) might suggest the slope of the growth curve is starting to decline (Figure 6), it is too soon to be sure.

Another dramatic example of species recovery by translocation is the Saddleback. Formerly widespread on the mainland, it disappeared there last century. The North Island subspecies became confined to Hen Island, but as a result of translocation now occurs on at least six other islands. The South Island subspecies was almost lost when ship rats decimated its last population on Big South Cape Island. Fortunately

enough were translocated to ensure its survival on several islands off Stewart Island. Other species becoming rare that have been translocated to increase their range and numbers include Little Spotted Kiwi, Brown Teal, Kakapo, Stitchbird, and Kokako, while captive breeding or rearing (with or without egg/brood manipulation) and release has been carried out on others, e.g. Yellow-eyed Penguin, Brown Teal, Takahe, Black Stilt and Antipodes Island Parakeet.

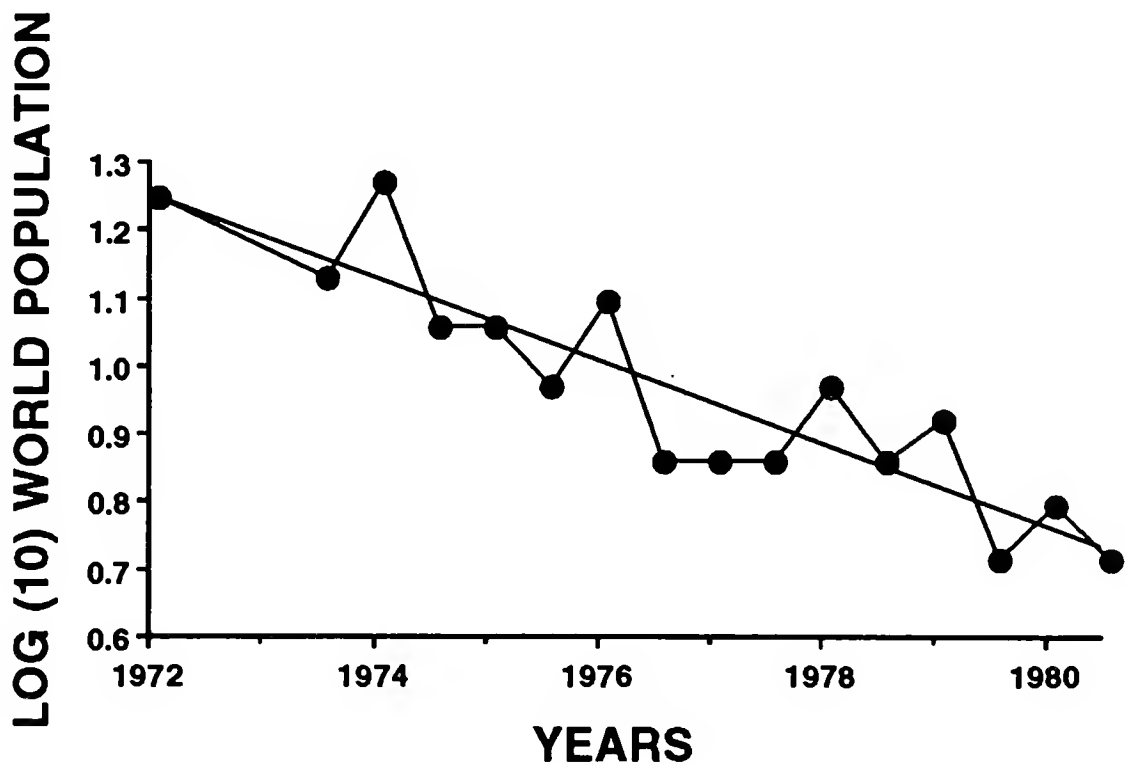


FIGURE 5 - Decline of Black Robin population. A log plot of population size is used to more clearly illustrate the trend towards extinction.

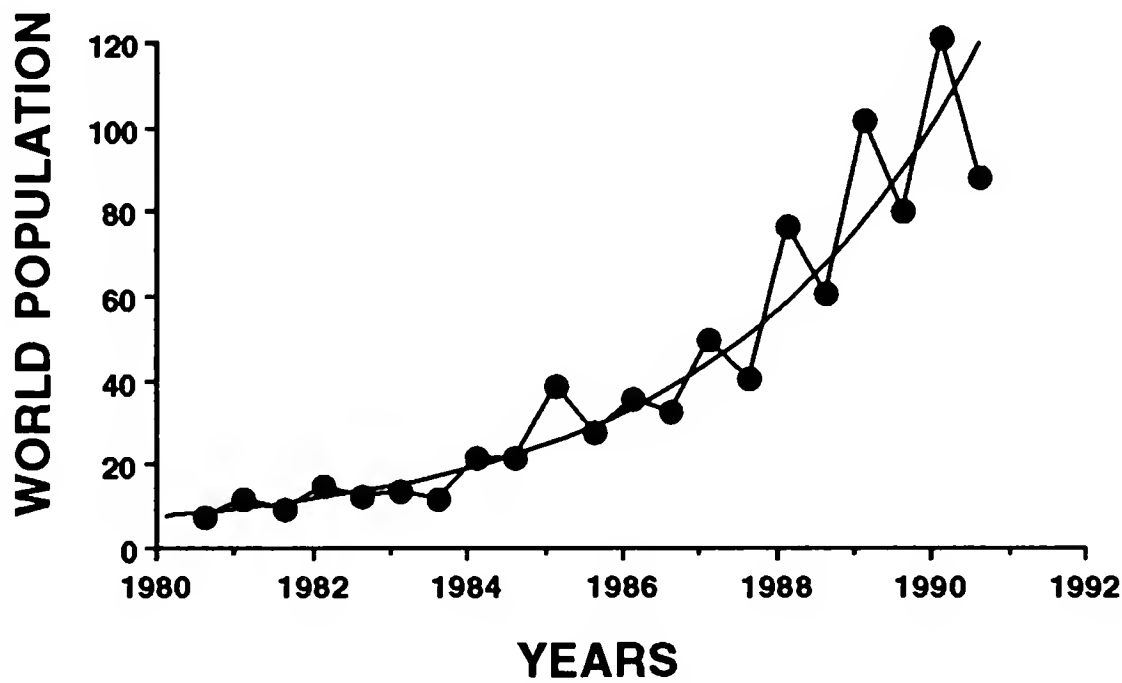


FIGURE 6 - Exponential recovery of Black Robin population. Note classical J-curve on this arithmetic plot of population size.

Extinctions

All species recorded extinct in New Zealand are non-marine birds. While many seabirds declined on the mainland and became locally extinct as breeding colonies, there are no recorded species extinctions of seabirds since human settlement. The Chatham Island Taiko, prominent in middens of the Chatham Island Moriori, was thought to be extinct until it was rediscovered by D. Crockett in 1978 (Harrison 1983).

LOSS OF NON-MARINE ENDEMIC SPECIES. About half of the 90 non-marine endemic species have been lost since human settlement (Figure 3). Only 46 (51%) are still extant, and many of them have reduced ranges and numbers. At least 35 (39%) were lost during the Polynesian phase of settlement, and a further 9 (10%) during European settlement. At least 44 species are, therefore, known to have gone extinct – 49 % of non-marine endemic species. This number of extinctions is likely to be an underestimate since more subfossil species may yet be described (P.R.Millener, pers. comm.). The number of bird species extinctions in different orders is shown in Figure 8. All 11 species of moas (Dinornithiformes) are extinct, while high extinction rates also occurred in the Anseriformes, Gruiformes and Passeriformes.

TABLE 5 - Extinction of New Zealand endemic species relative to different levels of endemism (excluding seabirds).

Level of Endemism	No. Taxa	No. Species	Extinct in Polynesian Phase	Extinct in European Phase	Total extinct	
					No.	%
Order	2	14	11	0	11	78.6
Infra-order	1	7	3	2	5	71.4
Family	2	5	2	1	3	60.0
Subfamily	4	7	0	1	1	14.3
Genus	19	23	10	2	12	52.2
Species	34	34	9	3	12	35.3
Totals	62	90	35	9	44	48.9

DATES OF EXTINCTION. Precise dates of extinctions during the Polynesian phase are not possible, so that the scenario presented in Figure 3 only provides a possible indication of past extinction trends. McGlone (1989) comments that “our knowledge of the impact of human settlement on the environment is still impressionistic and general, rather than quantitative and particular”. Estimates vary on the dates of moa extinctions. While Falla (1974) felt “it is probable that at least one of the smaller [species], the South Island bush moa *Megalapteryx* survived into the 19th century”, more recent assessments suggest moas died out much earlier, Caughley (1989) arguing their demise by 1400 AD - after “a brief passage in historical time, a wink in ecological time, and instantaneous in geological time”. Others propose somewhat later dates (King 1984, Holdaway 1989, McGlone 1989), with few left by 1450-1500. It is not possible to know precisely when the moas finally went extinct, but this was probably during the 16th century.

Even during the better documented European phase exact dating of most extinctions is difficult. The range of New Zealand taxa going extinct during the two phases of human settlement is shown in Figure 7. The following 9 species went extinct after 1800 (their last authenticated dates of survival are given in parenthesis): Stephens Island Wren (1894), NZ Little Bittern (1870-1900), Chatham Island Rail (1892), Chatham Island Fernbird (ca.1900), Auckland Island Merganser (1902), Huia (1909), Laughing Owl (1914), Piopio (1921) and Bush Wren (1965), information from Turbott et al. (1990) and Fleming (1982). More recent reports of some of these species re-

main unconfirmed, e.g. Laughing Owl, Bush Wren, Huia and Piopio (Fleming 1982). Subspecies disappearing since 1800 were the Little Barrier Snipe (ca.1870), NZ Quail (ca.1870), Macquarie Island Banded Rail (ca.1880), Chatham Island Bellbird (ca.1906), Macquarie Island Parakeet (1880-91), and Stewart Island Snipe (1965). The South Island Kokako seems very close to extinction (Turbott et al. 1990), if not already extinct.

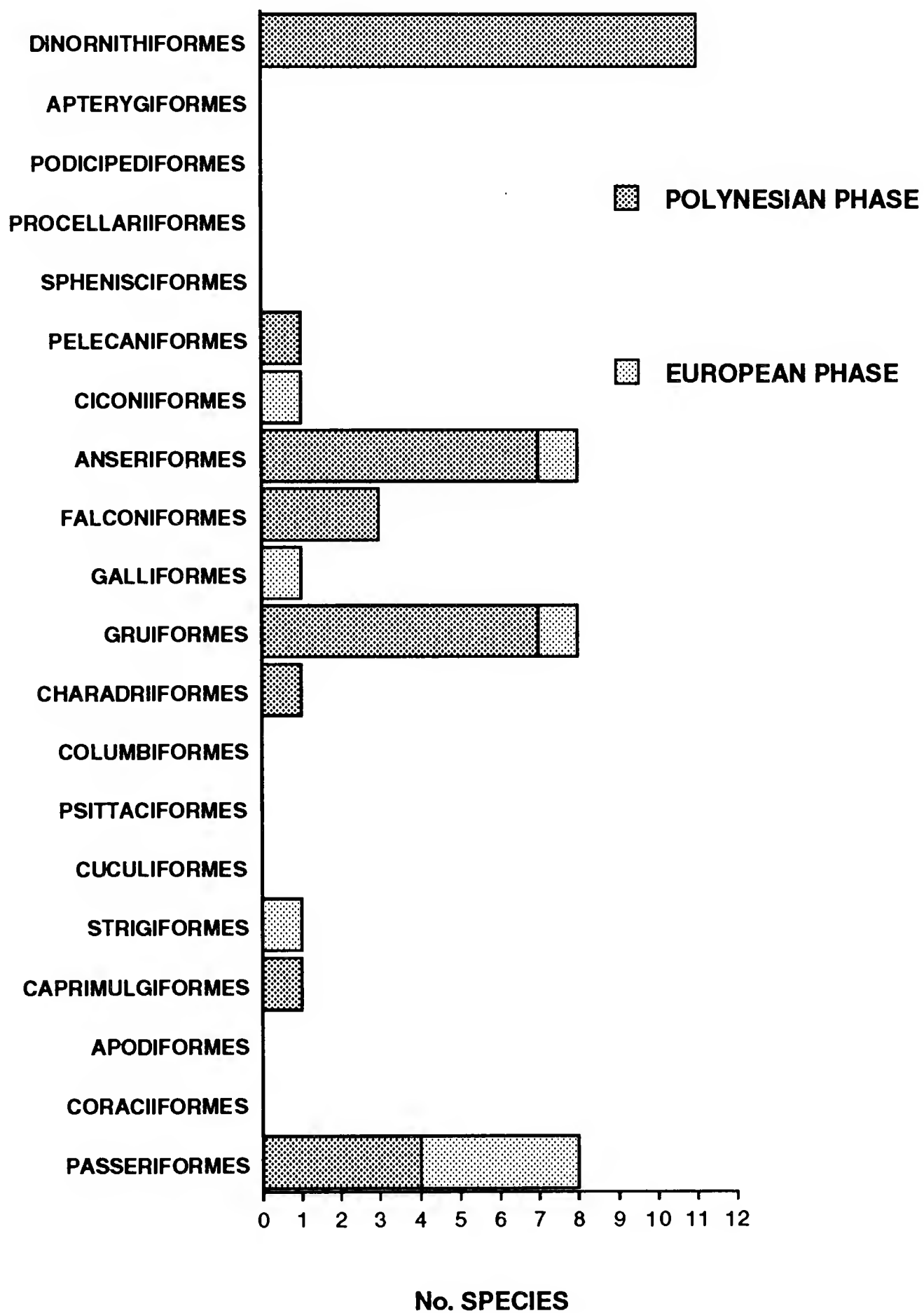


FIGURE 7 - Recent species extinctions in different orders of New Zealand birds.

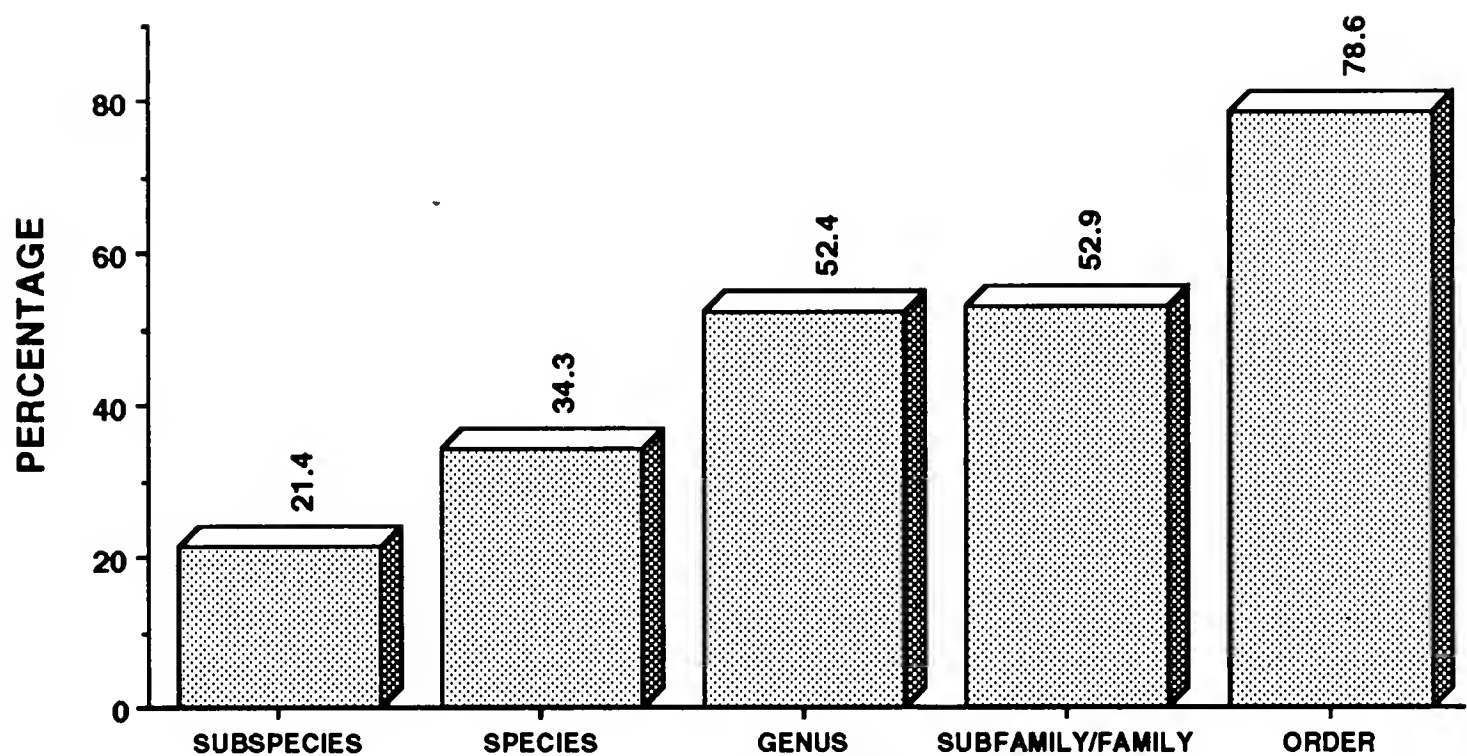


FIGURE 8 - Extinctions of non-marine New Zealand endemic birds in relation to different levels of endemism.

EXTINCTION IN RELATION TO LEVEL OF ENDEMISM. As McDowall (1969) noted, the general trend is for greater losses amongst those species endemic at higher taxonomic levels (Table 5, Figure 8).

MAIN CAUSES OF BIRD DECLINE AND EXTINCTION

Each of the three major human impacts - habitat change, hunting pressure and introduced biota - contributed directly to the decline and extinction of endemic birds. Holdaway (1989) notes that during the last 1000 years bird species became extinct at different times and rates depending on the particular aspects of their ecology and life history which made them vulnerable to habitat loss, hunting, predation, and competition for food resources. In turn, each of these factors embraces a wide range of situations, thereby adding to the multi-factorial nature of human impact on the avifauna and on the New Zealand biota in general.

Importance of habitat change

The severe reduction and fragmentation of forest would have directly reduced the range and numbers of New Zealand birds, progressively confining forest specialists to 'ecological islands' of forest remnants, and resulting in local extinction. Notwithstanding criticisms of island biogeography theory (e.g. Williams 1984), the direct empirical relationship between the size of such forest remnants and bird species number is well documented in New Zealand as elsewhere (Flux 1977, 1989, Hackwell 1982, Dawson 1984). With progressive fragmentation and reduction of forest areas the number of bird species follows a broadly predictable decline as populations become isolated and at greater demographic risk, with local extinctions occurring.

Conceivably this process alone may have ultimately led to the extinction of some species with specialised habitat requirements. Its major impact, however, would be to fragment and reduce the ranges and numbers of forest birds, through reduction of

ecological resources and population exchange within species. Such diminishing and localisation of species would have increased their vulnerability to the more potent pressures from human predation, and from predation and competition from the mammals that humans introduced. King (1984) notes the pre-European period saw many more forest bird species disappear than would be expected from the extent of deforestation alone.

On the positive side the modification of the New Zealand landscape into a mosaic of more open habitat types has led to an increase in the range of some species, such as the Australasian Harrier and NZ Pipit. It has also probably enabled other species to naturally establish which probably would not have been able to do so in former (forested) times - e.g. White-faced Heron, Spur-winged Plover and Welcome Swallow. Whether the Silvereye - now one of the most abundant of our forest birds - would have formerly established is a matter of conjecture. It is more likely to have done so than some other recent Australian colonists.

Before the arrival of humans in New Zealand the forests had a diverse range of native species - as Atkinson & Millener (1991) have illustrated - so that new forest adapted arrivals would not necessarily have gained a foothold. The relative lack of endemic species in mainland forests today might suggest plenty of niche opportunities for such colonists, but formerly these forests would have had a fuller complement of endemics. On relatively unmodified forest islands introduced passerines have not established as well as on the mainland. Diamond and Veitch (1981) noted this on Little Barrier Island, while on Big South Cape Island native species again predominated prior to their decimation by ship rats (Bell 1978, pers. comm.).

Importance of hunting pressure

There is abundant archaeological evidence that hunting pressure from Polynesians was a major factor in the decline and extinction of many endemic birds, including the 11 moa species (McDowall 1969, Cassels 1984, King 1984, Holdaway 1989, Millener 1990). Evolving in an environment lacking mammalian ground predators, they were likely to have been tame and relatively easy prey for Polynesian hunters. Sustained hunting pressure probably was the major factor in the decline of larger birds like all the moas and some other flightless species (Table 3). While smaller species, like the NZ Snipe and some forest passerines, were also hunted, they were generally less obvious or accessible so were unlikely to have sustained such substantial hunting pressure as the larger moas.

During the European phase of settlement, and especially during the nineteenth century, hunting pressure was maintained and the technology improved through the acquisition of firearms by Maoris as well as Europeans. The Auckland Island Merganser, with a similar form formerly also on the mainland (P.R. Millener, pers. comm.), probably went extinct directly as a result of hunting by Europeans (Fleming 1982). Again the Huia was eagerly sought by Maori and European hunters during its declining years (Fleming 1982, Galbreath 1989), though other factors, particularly mammalian predators, also contributed to its extinction.

Importance of introduced mammals

Both mammals brought by the Polynesians to New Zealand are likely to have had a dramatic impact on the endemic biota.

IMPACT OF KIORE. The kiore was a major predator of smaller fauna, depleting native birds numbers by both direct predation of adults, eggs, and young, and by competitively reducing available food resources. This rodent also probably had a major impact on other distinctive elements of the fauna, such as larger invertebrates and the herpetofauna (Atkinson 1978, Whitaker 1978, King 1984, Bell et al. 1985, Holdaway 1989). Holdaway (1989) notes the kiore's rapid 'blitzkrieg' colonisation probably accounted for many bird losses in the earliest stages of human settlement. He argued the most susceptible species disappeared over the first 200 years after Polynesian arrival due to the initial combined impact of hunting by Polynesians and dogs, and predation and competition for food after an explosive irruption of kiore. Vulnerable species probably included smaller ground birds like the Snipe-rail, the Stephens Island and Stout-legged Wrens, and, on the mainland, the NZ Snipe, as well as larger species such as the NZ Pelican, the *Cnemidornis* goose, the NZ Swan, Finsch's Duck, the NZ Musk Duck, Chatham Island Duck and the NZ Aptornis (Holdaway 1989).

IMPACT OF KURI. The kuri (dog) was in part a commensal of Polynesian settlements through to its disappearance when its identity became swamped by interbreeding with European breeds, though it was still recognisable in wild crossbreeds late into the nineteenth century (Thomson 1922). However, it seems likely that kuri would have dispersed away from human settlement to hunt native birds and other prey, particularly during earlier Polynesian settlement (until 1400-1500 AD) when such food would have been relatively abundant. Some have argued the kuri remained essentially a human commensal (e.g. Cassels 1984), given the lack of direct evidence (gnawed bird bones etc.). Others disagree (Anderson 1981, 1990, Holdaway 1989). It seems very unlikely that such a carnivore would not have had an impact on vulnerable bird species. As Anderson (1990) notes, even though kuri were capable of hunting ground birds, lizards, frogs, and insects, etc., their impact on the endemic fauna can not now be distinguished within the broader effects of human colonisation.

Although the size and extent of feral kuri packs is a matter of conjecture, recent evidence of dog predation suggests relatively few individuals can have a major impact on vulnerable New Zealand birds. Taborsky (1988) conservatively estimated a Brown Kiwi population in Northland was reduced by 500 birds out of a population of 900, following predation by a single female German Shepherd dog. He suggests it would take 10-20 years of rigorous protection to restore the Kiwi population to its former level. Again, stray pig dogs were responsible for decimating the remaining Little Spotted Kiwi populations of D'Urville Island in the early 1980s (Brian D. Bell, pers. comm.). Such observations of the impact of current breeds of domestic dog in New Zealand support the notion that the kuri would also have killed native birds and was likely to be a major factor in the extinction of some. Kuri are likely to have penetrated into areas less accessible to humans, so would have had an impact on remoter populations of endemic ground birds.

IMPACT OF MAMMALS BROUGHT BY EUROPEANS. During the European phase of settlement many more exotic animals were brought to New Zealand, including a wide range of mammalian predators and herbivores. As many have stated (e.g. Wodzicki 1950, Gibb & Flux 1973, Williams 1973, King 1984, Holdaway 1989) these mammals had a further detrimental impact on the endemic biota that had survived 800-1000 years of Polynesian settlement. King (1984) compared two periods of European settlement: the early European period (1769-1884) with arrivals of Norway rat, feral cat and the ship

rat (in the North Island only after the 1860s); the later European period (1884-present) with Norway rat, ship rat, feral cat, ferret, stoat and weasel as key mammalian predators. The various impacts of these predators have been (and continue to be) the major cause of the decline and extinction of endemic birds over the last 150 years. This has probably been mostly through direct predation of adults and progeny, though the indirect effect of reducing food resources may have added to the pressure on some species.

As though these predatory mammals were not enough, the native biota have also suffered the impact of a wide range of herbivorous mammals, mostly domestic and wild ungulates, though the marsupial brush-tailed possum has also had a major impact, particularly as an arboreal herbivore in mixed conifer-broadleaf forest (Wodzicki 1950, Bell 1981, King 1990). Some mammalian herbivores directly compete with endemic birds for food. For example, the decline of the Takahe is associated with red deer competition for favoured plant species in the Murchison Mountains (Mills & Mark 1977), while in the central North Island the diet of the brush-tailed possum overlaps with that of the declining Kokako (Fitzgerald 1984).

OTHER INTRODUCED BIOTA. In addition to introducing mammals, Europeans deliberately brought many more birds to New Zealand. Prominent among successful colonisers are European passerines, waterfowl and game birds. Many of these are now widespread and have successfully colonised the forests of the mainland and some off-shore islands. Their impact on endemic birds has not generally been overt, being more likely the result of exploitation competition rather than interference competition. However, concern has been expressed regarding interference competition by some species, such as the hole-nesting Eastern Rosella, Common Myna and Starling, or the nest-predating Australian Magpie.

Amongst exotic invertebrates the German wasp *Vespula germanica* and common wasp *V. vulgaris* have been cause for concern. As aggressive carnivores they are known to have a major impact on native invertebrates, probably affecting food resources of some insectivorous birds. They also compete directly with native honeyeaters and the kaka for honeydew, particularly in the beech forests of the South Island. Elliott (1990a) has implicated the German wasp as one factor in the decline of the Yellowhead, whose stronghold is now in relatively wasp-free areas of Fiordland.

Avian disease and parasites should be noted as relatively unknown factors in the decline of endemic birds in New Zealand. While the role of disease has been highlighted in the decline of many of Hawaii's endemic birds (Ralph & von Riper 1985), similar evidence accounting for the decline of New Zealand birds is wanting. While introduced predators top the bill as likely causes of avian declines, the possibility that introduced pathogens accelerated the sudden decline of some species over the past 150 years can not be dismissed. The epidemiology of avian disease, especially in threatened species, remains an under-developed area of research in New Zealand.

CONCLUSIONS. Polynesian settlement of New Zealand led directly to the extinction or reduction of much of the vertebrate fauna, destruction of half of the lowland and montane forests, and widespread soil erosion. The climate and natural vegetation changed over the same time, but had negligible effects on the fauna compared with the impact of settlement (King 1984, McGlone 1989). The extent of loss is not so

much a reflection of the Polynesian culture but rather that Polynesians happened to be the first humans to settle. Had Europeans arrived first then the losses may have been much more rapid.

Unfortunately the bird fossil record before the Holocene is poor and it is impossible to compare this extinction episode with previous ones (McGlone 1989). Nevertheless, it seems that the start of the extinction event after 1000-1200 BP. was relatively abrupt, and not part of a long decline (Cassels 1984) – i.e. it was due to substantially different ecological conditions brought about by human settlement. McGlone (1989) concluded that the human impact on the New Zealand biota and landscape “had eclipsed anything brought about by natural processes over the past 3 millennia”.

What is seen in New Zealand is also evident in other island biotas impacted by humans and their attendant animals - not least the numerous islands of the adjacent Pacific. While the size and isolation of many of these islands has resulted in a smaller land avifauna, the impact of human settlement has nevertheless been dramatic. Indeed many Pacific island endemic avifaunas are in a critical state and require urgent conservation if numerous species are not to disappear over the next few years (Hay 1986). New Zealand stands out in being a larger island archipelago than islands of the central Pacific, and has ancient land connections with the former Gondwana biota - as suggested by the continued survival of tuatara, some Leiopelmatid frogs and archaic invertebrates. Hence Diamond's (1990) reference to New Zealand as “one of the world's smallest continents . . . one of the world's biological prizes”. Compared with smaller archipelagos, humans and accompanying exotic mammals probably had a slower rate of impact in New Zealand, at least on the main islands (not on small islands, as illustrated by the Chathams Islands extinctions and the sudden loss of species on Big South Cape Island in the 1960's (Bell 1978)). Nevertheless, over time at least 49% of New Zealand's endemic land and wetland species have been lost. Millener (1990) notes “ The common conclusion derived from subfossil discoveries on . . . various oceanic island groups (with New Zealand no exception) is that prehistoric human interference has been profoundly adverse, with typically as much as 40% of the prehistoric avifauna having been extirpated within a few hundred years of first human settlement.”

HISTORY OF ORNITHOLOGY IN NEW ZEALAND

The Maori and ornithology

The Maori snared and caught birds for food, long bones and feather adornment. Important Maori food species during the early period of European settlement included forest birds (NZ Pigeon, Kaka, Tui, Bellbird, Weka, Kakapo and Kiwi), wetland species (Grey Duck, Pukeko, Paradise Shelduck) and seabirds (Sooty Shearwater, Fluttering Shearwater, Flesh-footed Shearwater, Black Petrel and Grey-faced Petrel). Again, Kiwi, NZ Pigeon (Kereru), Kaka and Tui were some of the species greatly valued for feathers, used in the decoration of feather cloaks (Prickett 1990). As an important prestige food to the Maori, birds were not just eaten when abundant but also for special occasions of group hospitality. Decorated gourd containers filled with preserved birds were stored in raised pataka (storehouses) ready for an occasion when “the laws of hospitality demanded the very best” (Prickett 1990). Birds became incorporated into Maori myths, traditions, art and language - many of New Zealand's

native species are today known by the Maori vernacular, either principally (e.g. Kakapo c.f. Owl-parrot, Kokako c.f. Blue-wattled Crow), or secondarily (e.g. Morepork c.f. Ruru, Yellow-eyed Penguin c.f. Hoiho). As with much of the biota, many birds are now typically known by three names - Maori, European (Pakeha) and scientific.

Clearly the avifauna of New Zealand has been dramatically influenced by the Maori who preceded the European arrivals of the eighteenth and nineteenth centuries. The science and pursuit of ornithology as we know it today stems from this later European (Pakeha) culture. While the Maori did not practise the science of ornithology in the literal sense, they did gain knowledge of avian diversity and behaviour through cultural association with birds. In this sense the Maori practised the "study of birds". Andrews (1986) notes "All man's relationships with nature – confrontational, passive, yielding - had been observed by the Maori, including the identification and observation of animals for their own sake. Even, by instinct or ritual, their conservation and management. But for the greater part the animals were recorded only in oral traditions, in stylised carvings, or in rock designs". Prickett (1990) notes "Traditional ethnological descriptions have the Maori living in harmony and balance with the natural world, including its birds (e.g. Best 1942) . . . exploitation of birds for food or other purposes demanded careful ritual and strict practical observances. Local control over resources, seasonal hunting, and rahui (a local ban over resource exploitation) are just some aspects of practical conservation practised by the Maori . . . It is easy to romanticise this ideal . . . careful exploitation of the new environment doubtless took time to develop . . . Maori exploitation of the environment was undoubtedly more responsible for, and responsive to, environmental change than the romantic view would represent".

Period of European discovery

EARLIEST EXPLORERS. Abel Tasman was the first European to visit New Zealand in 1642, but his visit contributed nothing to knowledge of the birds. However, Captain James Cook's three voyages from 1769 to 1777 "helped lay the foundations of New Zealand ornithology" (Fleming 1982). The ornithology of these voyages has been reviewed by Fleming (1982), Andrews (1986) and Medway (1990a).

COOK'S FIRST VOYAGE. Joseph Banks and Daniel Solander, with the artist Sydney Parkinson, were on Cook's first voyage on *Endeavour* (1768-1771). Unfortunately Banks and Solander did not publish the scientific results of that voyage, so its potential ornithological significance was not realised (Fleming 1982, Medway 1990a). The first documented New Zealand bird observation was on 7 October 1769 when, in Poverty Bay, Banks fired his musket at unidentified seabirds, possibly Fluttering Shearwaters or Cook's Petrel (Andrews 1986). A partly coloured drawing of an Australasian Gannet by Parkinson was the only New Zealand bird to be illustrated on this voyage. Most of the birds taken seemed to have been eaten (Andrews 1986).

DE SURVILLE'S VISIT. Jean de Surville in *St Jean Baptiste* landed in New Zealand for about two months in December 1769. He presented a pair of pigs and a cock and hen to the Maoris of Doubtless Bay. These were the first deliberate European introductions, but their fate is not recorded. The birds obtained by the expedition were not identified but may have included Tui and Pukeko (Andrews 1986).

COOK'S SECOND VOYAGE. Cook's second voyage on *Resolution* and *Adventure* (1772-1775) produced much more ornithological information. On board were Johann

Reinhold Forster and his son George, who were later joined by the Swede Anders Sparrman at the Cape of Good Hope. They collected assiduously at Dusky Sound and Queen Charlotte Sound. George Forster illustrated many species (Latham 1781-85, Sparrman 1787, Gmelin 1789). J.R. Forster described about 150 species of birds from the second voyage, but regrettably - from the viewpoint of New Zealand ornithology - the manuscripts remained unpublished until after his death. H. Lichtenstein of Berlin then produced them in 1844 under the title *Descriptiones Animalium* (Fleming 1982, Medway 1990a). Sparrman, after returning to Sweden, published Latin descriptions and names of 9 New Zealand birds in his *Museum Carsonianum* (1786-89): Spotted Shag, Western Weka, Red-crowned Parakeet, Long-tailed Cuckoo (taken in Tahiti), South Island Rifleman, South Island Fantail, South Island Robin, Bellbird and South Island Piopio (Medway 1990a).

The long delay of almost 70 years before publication of J.R. Forster's work in 1844 meant other workers, quite unfamiliar with the species in their natural habitats, were able to describe and validly name them first. Consequently few species are now known by the names given them by Forster in *Descriptiones Animalium*. Exceptions are Fluttering Shearwater, Mottled Petrel, Red-billed Gull and Variable Oystercatcher (Medway 1990a).

Five geese were introduced at Goose Cove during Cook's second voyage and other animals set foot on land briefly, such as sheep and goats which were put ashore only for the duration of the visit, while a cat and dog also had brief periods ashore. The Norway rat *Rattus norvegicus* probably arrived at this time, or on Cook's other voyages, though a lesser possibility of ship rats *R. rattus* being carried on board also remains (c.f. Andrews 1986). If not Cook, then later whaling and sealing vessels may have brought Norway rats before the turn of the century (Innes 1990, Moors 1990), but the house mouse *Mus musculus* probably came later (Murphy and Pickard 1990).

COOK'S THIRD VOYAGE. William Anderson, surgeon on Cook's fatal third voyage on *Resolution* and *Discovery* (1776-1779), made significant ornithological observations in his journal and zoological manuscripts, illustrated by W.W. Ellis, (Fleming 1986, Medway 1990a). John Latham made extensive use of Anderson's manuscripts when compiling his *General Synopsis of Birds* (1781-1801). However, he only used English names for the new species described from New Zealand, and it was Gmelin in his edition of *Systema Naturae* (1788-93) who translated them into short Latin diagnoses and so has credit for formally describing many new species. Sir Joseph Banks was the main recipient of the ornithological specimens collected on Cook's three voyages, but these became dispersed and few survive (Medway 1990a). During Cook's third voyage further mammals were released in New Zealand: "pairs of goats and pigs here, and also two pairs of rabbits; other animals made a brief appearance - horses, cattle, sheep, goats, turkeys, geese, ducks and a peacock" (Andrews 1986).

LATER EXPLORATIONS. Only a sketchy zoological narrative comes from the later British visits of Vancouver in *Discovery* and Brougham in *Chatham* late in 1791 (Andrews 1986). Later explorers contributing ornithological knowledge included the Frenchmen Crozet, Duperrey, Lesson and Dumont d'Urville. Three expeditions visited over 1840-41: d'Urville with *L'Astrolabe* and *La Zelee*, Wilkes of the American Exploring Expedition with Titian Peale (1840), and the British expedition of Sir James Clark Ross in *Erebus* and *Terror* (Fleming 1982).

The rough and tough gangs of sealers and whalers worked New Zealand waters during the last decade of the eighteenth century and the early nineteenth century. As Andrews (1986) notes: "On the face of it, the contributions of these gangs to natural history were negative ones, but now and then . . . would come one or two spectacular zoological offerings . . ." One such offering was the skin of a most unusual bird which was brought by Andrew Barclay to London, where it reached the hands of W. Evans who worked in the British Museum. The first account of this bird - the Brown Kiwi - was in Shaw and Nodder's *The Naturalist's Miscellany* . . . (1813), with a strangely elongate illustration based on the skin (Andrews 1986). So it was that news of the first specimen of New Zealand's national bird reached the scientific world. Despite suspicions the bird might be a freak, corroboration of a small "Emu-like" bird in New Zealand soon followed, though it was not until Yarrell re-examined the original skin in 1833 that a more credible illustration by John Gould was produced. From 1835 more specimens arrived in London, but it took 40 years after the first discovery before a live kiwi reached the Zoological Society in London in 1851 (Andrews 1986).

Nineteenth century collection and discovery

European settlers of New Zealand - which gained its nationhood following the signing of the "Treaty of Waitangi" in 1840 - were initially preoccupied with the practical challenges of 'taming' a substantially forested country to one of settlements, roading and pastoral development. The 1840s and 1850s were times when bird observations and collection increased, with most published reports appearing overseas. Locally published accounts of native birds did not generally appear until later in the century (Fleming 1982). Observers of New Zealand ornithology during the greater part of the nineteenth century not only became familiar with the native birds but bore witness to their rapid decline towards the century's end. At the time that the "Treaty of Waitangi" was signed (1840), a good half of the land was still in native forest, and a wide and vocal range of species could still be encountered on the mainland - including kiwis, Kaka, Red-crowned Parakeet, Yellow-crowned Parakeet, Bush Wren, Robin, Stitchbird (North Island), Saddleback, Kokako, Huia (North Island) and Piopio - all much reduced or extinct today. The NZ Quail was reported to be extremely abundant in some areas in the 1840s, such as the open plains of the South Island, but it was gone by 1869 (King 1984).

SPECIMEN COLLECTING. In contrast to present day attitudes, the prime goal of many of the nineteenth century ornithologists was to secure specimens of native birds. These were not only collected for science and the world's major museums, but were obtained for private collections, such as those of Rothschild in England (Galbreath 1990a). The rarer the species, the greater the demand, with the inevitable consequence of hastening the extinction of the rarest species. A veritable trade in native species developed, the collectors cashing in on the financial and scientific rewards of the day - indeed by 1880 there was something of a glut on the market - one London dealer declining any more New Zealand birds, having about 385 Kakapo and upwards of 90 Little Spotted Kiwi for disposal. Even the recipients at times complained - for instance in 1895 Rothschild wrote to Buller explaining he did not want any more Stitchbirds (Galbreath 1989).

Particularly vulnerable were rarities confined on some islands. On the Chatham Islands over 1872-95, collector William Hawkins provided "a matchless series" of the Chatham Island Rail for the Hon. Walter Rothschild's collection immediately prior to

its extinction (Fleming's 1982 description); again, local lighthouse-keeper Lyall saw that H.H.Travers was supplied with specimens of the Stephens Island Wren during the year of its discovery and extinction; these went to the collection of Rothschild, Lyall getting the species named after him (*Traversia lyalli*). Less easy to track down were some of the mainland species, which were already facing the onslaught of habitat loss, introduced predators, competitors and possibly disease. Without doubt intensified collecting was the last straw in the demise of the magnificent Huia, a NZ wattlebird (Callaeidae) with sexual dimorphism of its bill and apparently cooperative feeding between the male and female.

The Huia had a special significance for the Maori, who greatly prized the large black, white-tipped tail feathers (King 1984). Despite this, both Maori and European traded in Huia skins and continued to do so until its extinction early this century. Over 600 Huia skins resulted from an expedition to the Tararuas in 1874. Local Maori chiefs had prohibited Huia hunting in the area for the previous seven years in the hope this would arrest their continued slaughter (King 1984). Prevailing attitudes are evident from the following two quotes: Ernst Dieffenbach (1843) on a trip made near Wellington in 1839 - "I added to my collection a very curious bird . . . the continued shrill whistling of my guide, *Uia. Uia. Uia* . . . had attracted four . . . I fired and killed two or three of them"; and Walter Buller in 1892 - "To show how much scarcer this bird is than it was formerly . . . during the whole expedition we saw only a single Huia - which I shot - a male bird . . . in these ranges only five or six years before the Huia was comparatively plentiful".

While reprehensible in the light of today's enlightened conservation attitudes, the fervent collecting of native birds in New Zealand did contribute much to ornithological science through the provision of specimens for study, particularly in the museums and private collections of Europe.

GEORGE ROBERT GRAY. In 1842 the Directors of the New Zealand Company presented the British Museum with 37 specimens of birds collected by their naturalist in New Zealand, Ernst Dieffenbach, over 1839-41. These, together with other material and collections (e.g. those of Rebecca Stone and Andrew Sinclair), were worked on by George Robert Gray (1808-1872) who produced the first checklist ('List of the birds hitherto recorded in New Zealand, Chatham and Auckland Islands, with their Synonyma', pages 186-201 in Dieffenbach, E. (1843) *Travels in New Zealand*). Gray considered 8 of the 84 listed names to be new, and five of them still apply (Medway 1990b). Gray continued to publish New Zealand ornithological material, including bird sections in *The Zoology of the Voyage of HMS Erebus & Terror* (1844-1845), his *Genera of Birds* (1844-49), a description of the Kakapo (1847), his *Catalogue of the Genera and Sub-genera of Birds* (1855), and 'A list of the birds of New Zealand and the adjacent islands' in *Ibis* (1862). Medway (1990b) sums up Gray's contribution thus: ". . . there can be no doubt that Gray, although he lived in London and saw alive none of the many New Zealand birds he described, made by far the most significant contribution of his time to the taxonomy of the New Zealand avifauna".

ANDREAS REISCHECK. Another prominent collector was the Austrian Andreas Reischek (1845-1902). in the words of Westerskov (1990b) his ". . . major achievement was undoubtedly his large and almost complete collection of New Zealand birds, one of the best in existence and now well preserved in the Vienna Museum of Natural His-

tory". He added three birds to the New Zealand list - the Black-footed Albatross, the Antipodes Island race of the Red-crowned Parakeet (Reischek's Parakeet) and the Antipodes Island race of the NZ Pipit (Westerskov 1990a,b). His shooting of 150 Stitchbirds on Little Barrier Island during the 1880s, at a time when the species had gone extinct on the mainland, has given his collecting some notoriety (Fleming 1982, Andrews 1986).

MOA DISCOVERY. The moas of New Zealand were not brought to the attention of the scientific world until well into the nineteenth century. Andrews (1986) attributes the first account of moa bones to Joel Polack in 1838, the first bones eventually reaching the hands of Professor Richard Owen at the Royal College of Surgeons in London in 1839. Owen's identification as "an unknown struthious bird of large size, presumed to be extinct . . ." appeared in the *Proceedings of the Zoological Society of London* in 1840. Owen then "established himself as the logical ultimate receiver of Moa bones" (Andrews 1986) and dominated the early publications on moas.

BULLER AND POTTS. Among nineteenth century New Zealand ornithologists, two men, Sir Walter Buller (1838-1906) and Thomas Henry Potts (1824-1888), stand out (Galbreath 1990b,c). Buller's *A History of the Birds of New Zealand* was a landmark publication in New Zealand ornithology. The first edition, with hand-coloured lithographs from paintings by J.G. Keulemans, appeared in 1873. An enlarged second edition followed in 1888, and a *Supplement* in 1905. These volumes, especially the second edition, became the standard work on New Zealand birds until W.R.B. Oliver's *New Zealand Birds* in 1930 (Fleming 1982).

T.H. Potts contributed to New Zealand ornithology through his writings on the native forests and bird-life, such as articles published in the *New Zealand Country Journal*. His accounts of the habits of birds of his time - some now extinct - provide a valued record and they contrast with the grander style of Buller and his reference to procurement with the gun. Potts was a keen advocate for bird protection.

ACCLIMATISATION ACTIVITY. Much effort during the latter part of the nineteenth century was towards the settlement of new exotic species, like many common European species, or the controversial stoat and ferret brought in to counter another exotic - the rabbit. Regional Acclimatisation Societies were established to foster and implement the introduction and spread of these new species to New Zealand. An Auckland Acclimatisation Society was formed in 1861, followed by societies in Nelson (1862), Canterbury and Otago (1864). There was little official control over importations. The Protection of Certain Animals Act 1865 and its successor 'an Act to Provide for the Protection of Certain Animals and for the Encouragement of Acclimatisation Societies in New Zealand 1867' prohibited fauna like raptors and venomous snakes, and protected native species that could be regarded as game (Andrews 1986).

EMERGENCE OF CONSERVATION AWARENESS. The dramatic loss of forest habitat and the decline of native birds during the nineteenth century, together with the determined collectors' exploitation of remaining rare species, caused some protest, though such views were initially in the minority and not readily accepted by some of the scientific community in New Zealand. Those arguing for bird preservation had to battle the prevailing attitude that loss of forests and birds were inevitable - a view which provided justification for the continued exploitation of native birds. For some species extinction

may indeed have been inevitable, given the loss of habitat and the increasing numbers of introduced predators and competitors. However, this was not the case with all endemic species, as evident by those surviving today.

Despite difficulties, moves to protect native birds gradually gained momentum towards the century's close. Visitors such as Hochstetter had sounded warnings on the depletion of the fauna, and "early issues of the *Transactions* carried the rumblings of local naturalists against the follies of plundering animal life and haphazardly introducing foreign species" (Andrews 1986). In 1868 T.H. Potts moved in Parliament that steps should be taken "to ascertain the present condition of the forests of the Colony, with a view to their better conservation". The idea was not taken seriously (Galbreath 1989). Before the turn of the century, however, scientists, naturalists, and interested laymen, working through the incorporated societies of the New Zealand Institute, had begun to urge Government to set aside reserves (Fleming 1982). The Government first reserved Resolution Island and then Little Barrier Island as native bird reserves (as a result of the Onslow memorandum, drafted by Buller). The case for government protection of New Zealand birds, including legal protection for the Huia, as set out in Governor Onslow's memorandum of 1892, was not based on New Zealand viewpoints, but on the "dictates of prominent British zoologists. Men such as Newton and Sclater . . . had "over and over again urged the importance of some steps being taken for the conservation of New Zealand birds" (Galbreath 1989). The Onslow memorandum argued that birds such as the Kiwi and Kakapo should be moved to safe islands from the mainland.

Kapiti Island was added as a further reserve and later the Government sought the end of pastoral leases on the Subantarctic Islands (Fleming 1982). While the Huia was eventually gazetted as a protected species in February 1892, Buller worked to procure specimens for Rothschild, the Governor's wife (Lady Onslow) and himself right up to the legislation taking effect, and beyond (Galbreath 1989). Towards the end of his life, Buller in his *Supplement* took a more righteous stand on conservation policies then haltingly gaining acceptance, when his own collecting was virtually over (Bagnall 1966, Fleming 1982). Little Barrier and Kapiti Island are still important bird reserves today. However, stoats reached Resolution Island effectively wiping its sanctuary status, despite Richard Henry's pioneering attempts at relocating birds from the mainland at the turn of the century - in vain he moved hundreds of Kakapo, as well as Brown Kiwi and Little Spotted Kiwi, there over 1895-1907 (King 1984, Atkinson 1990a). The Animals Protection Act of 1911 declared practically all native species to be protected. A revised Animal Protection Act was passed in 1921-21 (Fleming 1982).

Twentieth century ornithology in New Zealand

The developments of ornithology in New Zealand this century are covered by Fleming (1982), Gill & Heather (1990), and particularly by Gibb (1990).

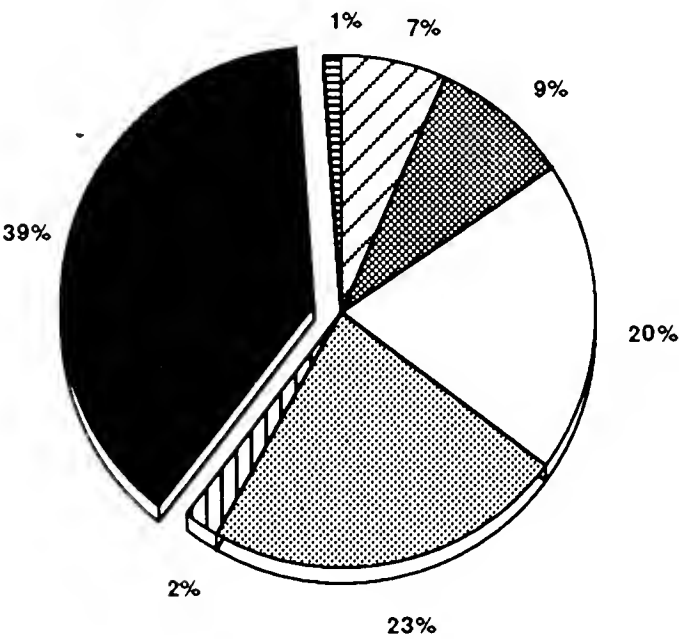
ORNITHOLOGICAL PUBLICATIONS. The major ornithological work following Walter Buller's *Supplement* (1905) was W.R.B. Oliver's *New Zealand birds* (1st edition 1930, 2nd edition 1955). This is still a standard work and immediately provided a stimulus for bird study (Turbott 1990). Prior to Oliver's book, reference had to be made to Buller, or to such works as Hutton & Drummond's *Animals of New Zealand* (1904), Guthrie Smith's various books (1910-1936), or Perrine Moncrieff's *New Zealand birds and how to identify them* (1925). Other contributions include G.M. Thomson's *The naturaliza-*

tion of animals and plants in New Zealand (1922), E.F. Stead's *Life histories of New Zealand birds* (1932), and E.G. Turbott's *New Zealand bird life* (1947). More recently the *Field guide to the birds of New Zealand* (Falla, Sibson & Turbott 1966, revised 1979) has become the standard field guide, while a substantial contemporary reference work is the *Reader's Digest Complete book of New Zealand birds* (Robertson 1985). C.A. Fleming's *George Edward Lodge - The unpublished New Zealand bird paintings* (1982) provides a valued combination of excellent art work with informative commentary on the avifauna. This book also addresses aspects of the history of ornithological discovery, as do John Andrews's *The southern ark - Zoological discovery in New Zealand* (1986) and Ross Galbreath's *Walter Buller - The reluctant conservationist* (1989). Harper and Kinsky (1978) provide an identification guide to Southern albatrosses and petrels, covering mostly New Zealand species. Checklists are provided by Fleming et al. (1953), Kinsky et al. (1970, with additions and amendments in 1980), and Turbott et al. (1990).

ORNITHOLOGICAL RESEARCH. Serious ornithological study in New Zealand has attracted both the professional and amateur. Centres for ornithological research have been the universities (which now number seven), major museums (Auckland, Wellington, Christchurch, Dunedin), and a varied range of government departments. Up to recent years government bird research had been carried out by the former NZ Wildlife Service and by the former Ecology Division of the Department of Scientific & Industrial Research (DSIR), with other inputs from the former New Zealand Forest Service's Forest Research Institute. Over recent years government restructuring has led to the new Department of Conservation becoming the major government Department associated with bird research and management, while Ecology Division DSIR has now been absorbed into a new division - DSIR Land Resources. The former NZ Wildlife Service deservedly gained high international recognition and profile for its efforts to conserve the nation's most endangered birds - as evidenced by the successes with the Black Robin, Saddleback, Black Stilt and Takahe (Adams 1990). Again, the former Ecology Division of DSIR gained a high reputation for its research on the ecology of native and introduced biota, including both native and pest species of birds (Robertson 1990). Until the 1960s, ornithology received little attention in the universities except for Otago (Gurr 1990). Thereafter, with an increasing move in curricula away from comparative morphology towards teaching with ecological and systems emphasis, more universities moved into the field of bird research. Ornithological research by university staff and graduates grew steadily, and today Auckland, Massey, Victoria, Canterbury, Lincoln and Otago contribute to the field, especially in the area of avian behaviour, ecology and conservation (Gurr 1990).

In a nation supporting so many rare and endangered species, it is not unexpected that a considerable emphasis today is towards bird conservation, either directly (in relation to management of threatened birds, habitats or pests), or indirectly (data collection, survey and species monitoring). That strong conservation emphasis is evident in the cooperative organisation of the 20th International Ornithological Congress and the 20th World Conference of the International Council for Bird Preservation, under the common theme of "The World of Birds - a Southern Perspective". Such an emphasis is again evident in the distribution of papers presented by New Zealanders compared with overseas participants at this 20th Congress (Figure 9), and in the institutions with which New Zealand members of the Congress are associated (Figure 10).

NEW ZEALAND CONTRIBUTIONS



OVERSEAS CONTRIBUTIONS

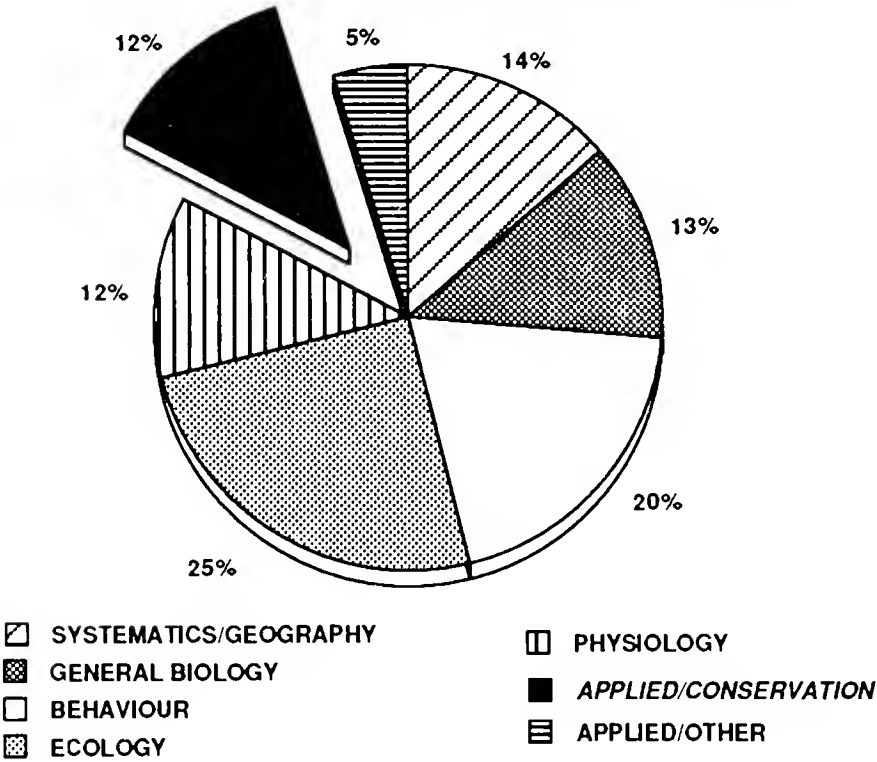


FIGURE 9 - Distribution of papers from New Zealand and overseas participants at the 20th International Ornithological Congress, compared in relation to major ornithological themes of the Congress.

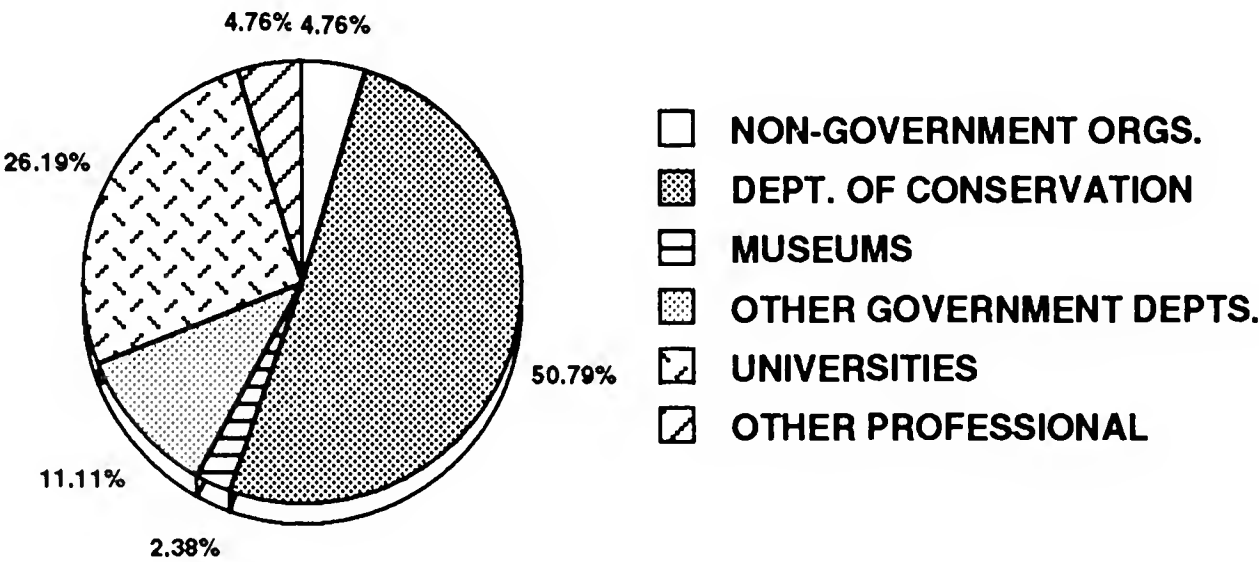


FIGURE 10 - Institutional origins for New Zealand members of the 20th International Ornithological Congress (private addresses excluded).

Conservation-oriented research and management seems likely to continue to dominate New Zealand ornithology for the immediate future. While the sixties and seventies saw an increase in ecological and behavioural studies of birds, over recent years there has been a growth in the application of biochemical studies (gel isozyme electrophoresis and DNA techniques) in the fields of avian systematics, population genetics and conservation (see Triggs and Daugherty 1990). Other current areas of research include avian physiology (energetics, flightlessness, endocrinology - see Cockrem 1990), avian vocalisations (song repertoires, dialects, evolution - see Jenkins 1990) and applied ornithology (pest species e.g. introduced finches, sparrows, starlings and corvids, or rare and endangered species).

ORNITHOLOGICAL SOCIETIES. The joint participation of amateur and professional ornithologists has been fostered through the activities of ornithological societies in New Zealand. The first ornithological society to be established in the region was the Royal Australasian Ornithological Society in 1901. The RAOU covers both Australia and New Zealand, having its main centre of activity in Australia. The Royal Forest and Bird Protection Society (RFBPS) was founded in 1923 as the 'Native Bird Protection Society', largely over concern at the state of Kapiti Island - a similar society had been briefly active in 1915 (Fleming 1982, Hutching 1990). Today it is New Zealand's largest conservation organisation with a membership exceeding 50,000. Hutching (1990) reviewed its recent achievements regarding bird conservation, involving such birds as Black Robin, Black Stilt, Kokako, Kea, Yellow-eyed Penguin, Blue Duck, Yellowhead and NZ Dotterel. Its journal *Forest & Bird* provides an informative commentary on current conservation issues.

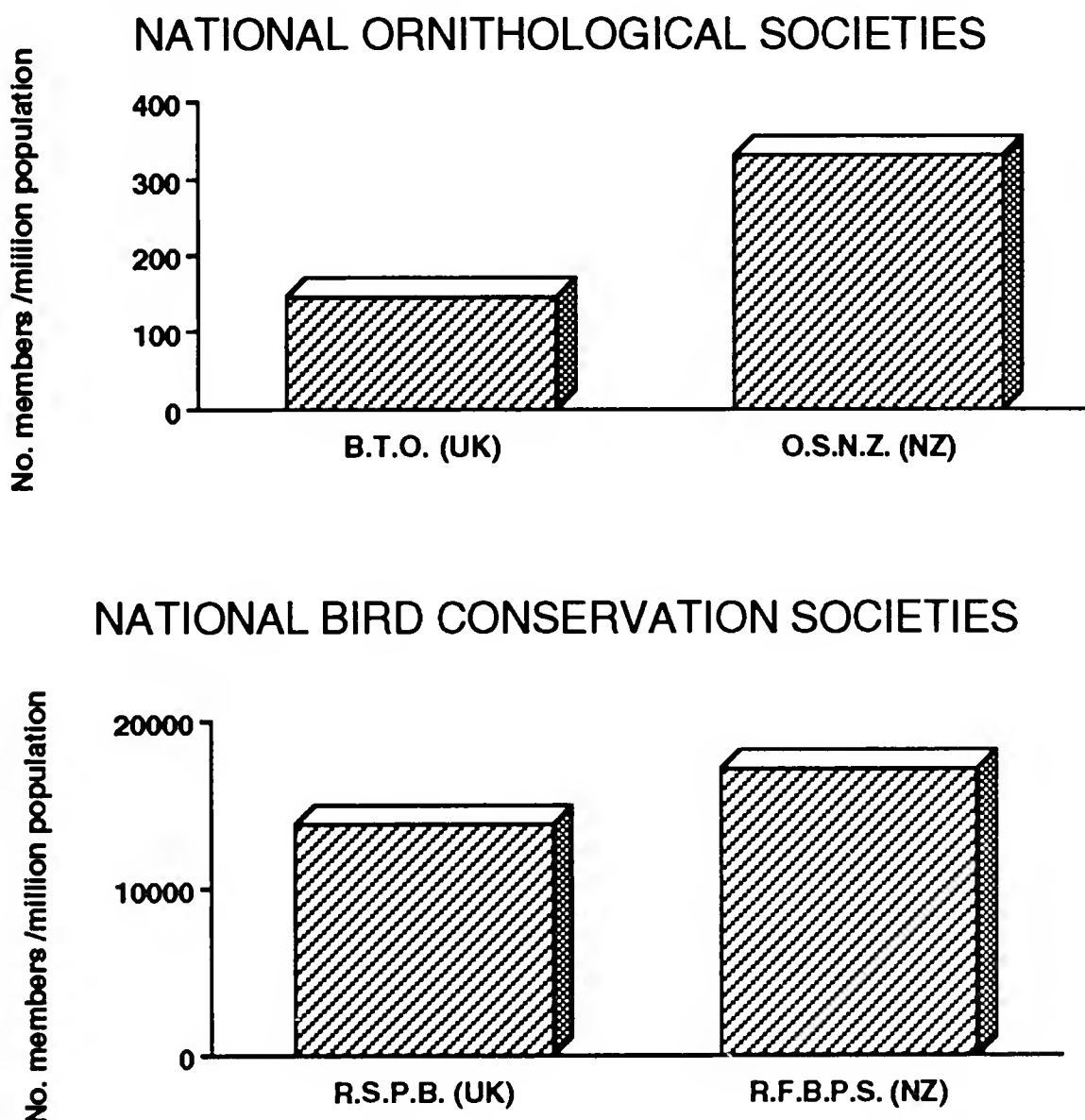


FIGURE 11 - Membership of national bird societies in Great Britain and New Zealand, expressed as a proportion of the human population of each country.

The Ornithological Society of New Zealand (OSNZ) was established in 1940, steered into being by Professor Brian Marples, Professor of Zoology at Otago University, who had emigrated from Britain in 1937 (Gill 1990). Its quarterly journal *Notornis* is a major outlet for New Zealand ornithological research. Since 1976 a more informal newsletter *OSNZ News* has been produced. With a membership exceeding 1000, the OSNZ promotes a range of national ornithological investigations, such as the nest record scheme, the beach patrol scheme, the moult scheme, wader counts and the bird atlas scheme; also shorter-term projects focussed on particular species. A fuller account of its activities and history appears in its jubilee publication *A flying start* (Gill and Heather 1990). Other important Society publications are *The new guide to the birds of NZ* (Falla, Sibson & Turbott 1979; first published 1966), *The atlas of bird distribution in NZ* (Bull, Gaze & Robertson 1985), the *Checklist of the birds of New Zealand* (Turbott et al. 3rd edition 1990) and *Fifty years of bird study in NZ* (Heather & Sheehan 1990). The Society is a major sponsor of this 20th International Ornithological Congress. The RFBPS and the OSNZ have continued to grow and prosper. Expressed as a proportion of the total population, they fare rather better for membership than do their counterparts in Britain (The Royal Society for the Protection of Birds and the British Trust for Ornithology - Figure 11), although in absolute terms the level of the New Zealand memberships is, of course, much less.

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PLENARY LECTURE

COMMUNAL BREEDING ALONG THE
CHANGING FACE OF THEORY

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COMMUNAL BREEDING ALONG THE CHANGING FACE OF THEORY

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ABSTRACT. The way behavioural scientists including ornithologists, approach science is often blinkered by an uncritical acceptance of theory, by their culture and by the characteristics of their study species. The history of studies of communal breeding birds provides a good illustration. This paper will attempt to follow the study of these birds as an example of how the questions asked and the evolutionary solutions offered vary with current understanding of theory. Birds grouped as communal breeders are a disparate group that varies widely from largely monogamous pairs with occasionally retained young, through to communally and incestuously mating polygynandrous groups. Some are migratory, some are colonial. Studies prior to the rise of sociobiology and inclusive fitness theory in the 1970s were largely of natural history. Subsequently researchers have used long term studies of communal breeders to argue for and against altruistic behaviour, kinship theory, inbreeding avoidance, parental investment and other theoretically topical ideas. Workers within the field have increasingly challenged the views of others and the recent criticism of the panselectionists claims of sociobiology has quickened the pace of re-evaluation.

Keywords: Communal breeding, helping, theory, pluralism, multifactorial, null model, kinship, familiarity, inbreeding

INTRODUCTION

When doing science the types of question we ask, the methods we use and the variables we measure are all derived from theory. The usefulness of theory is subsequently evaluated by consensus views on how well observations and measurements are explained and predicted. Many times theory appears to perform well, but how often is this a consequence that no realistic alternative was tried?

While many conferences attract researchers of similar mindset, a large international conference based on our taxonomic division of animals will assemble a range of theoretical approaches. Even though the presentation of seemingly non-comparable data sets and conflicting explanations will then lead to a healthy questioning of theory, without a theoretical framework our data will be even less useful as the following quotes demonstrate.

"Science cannot be carried on effectively by intelligent ignoramuses. Purely objective, unbiased collection of raw data is a myth that has distorted our understanding of science for long enough. Scientists cannot wipe their minds clean. Even if they could, they would be unwise to do so" (Hull 1988).

"The scientific literature is overwhelmed by reportage of observations that are published merely as observations without organic relationship to precisely formulated hypotheses. Such observations are scientifically meaningless. They are boring and soon to be forgotten" (Eccles in Dayton 1986).

Theory can be most useful if we adopt a pluralists view (c.f. Gray 1988, Wilson 1989) whereby the only value ascribed to theories relates to whether they add new aspects to explanations of nature. Theories are useful as tools for biologists but have no intrinsic value (e.g. Gray 1988) yet many biologists often appear more intent on supporting theory than describing or explaining nature.

In addition to providing suggestions for increasing our understanding of communally breeding birds I have two aims. Firstly I wish to reinforce the idea that our perceptions differ and hence so do the questions we ask, and secondly I wish to stress the advantages of a multifactorial and pluralistic approach to biology.

COMMUNAL BREEDING

Communal (or cooperative) breeding is a reproductive system in which one or more members of a social group provide care to young that are not their own offspring. These care givers are typically non-breeding adults called "helpers" or "auxiliaries" or they may be joint breeders sharing with other reproductive adults (Stacey & Koenig 1990). The use of the terms cooperative and helper is unfortunate as both imply a motivation which reinforces conventional selection-based explanations and hence may limit the consideration of alternatives. The latter term is now so widespread that I retain its use however.

Birds grouped as communal breeders comprise a disparate group that vary greatly in their behaviour and life history patterns (Brown 1987). They include seemingly monogamous pairs that occasionally retain young through to permanent groups that mate both incestuously and polygynandrously. A small number are migratory, some are colonial while the majority hold year round group territories. Good descriptions are provided elsewhere (eg. see Emlen 1984, Woolfenden & Fitzpatrick 1984, Brown 1978, 1987; Koenig & Mumme 1987, Stacey & Koenig 1990).

FACTORS INFLUENCING OUR SCIENTIFIC PERSPECTIVE

As Hull (1988, see above) has suggested, scientists do not approach data collection with uncluttered minds. We are all influenced by the prevailing scientific culture of our institution and associates. This in turn is influenced by our past interactions as well as familiar geographic patterns in nature. The different ways that we each perceive science and nature are important for developing a greater understanding of communal breeding and we can further communication by a greater awareness of our personal biases.

Geographic influences

Less than 3% of over 9000 species of birds in the world are known to breed communally but the numbers will grow as intensive studies of banded birds increase (Brown 1987, Emlen 1984). Of the 220 communal species, the majority are from tropical and warm temperate areas especially south of the equator. The overwhelming dominance of cold temperate and especially continental Northern Hemisphere science ensured that the phenomenon remained largely neglected until the late 1960s.

Skutch (1935, 1961, 1987) is the person commonly credited with first directing world attention to communal breeding or "helpers at the nest" to use his term. He suggested that it was the prevailing theory which assumed breeding territories were held by a single pair which led to the neglect of communal breeding. Rowley & Russell (1990) suggested that communally breeding birds behave similarly to humans yet many Northern Hemisphere workers express surprise at the phenomenon. For Rowley, the

remarkable thing is that the classical pair-breeding species shed their young so quickly.

Brown (1987) suggested that the neglect of communal breeding was partly a geographic phenomenon among scientists; that until recently the overlap between scientists and communally breeding birds was limited. Brown may be partly correct but the perceptual and theoretical bias suggested by Skutch & Rowley appears real.

In New Zealand, long before Skutch's 1935 paper and before earlier Northern Hemisphere papers such as Leach (1925), naturalists were reporting communal breeding without special comment. Guthrie-Smith (1910) recorded more than one female laying in the same nest plus group rearing of young among Weka *Gallirallus australis* trios and among larger groups of Pukeko *Porphyrio porphyrio melanotus*. He also noted older chicks feeding younger ones among Pukeko. Guthrie-Smith (1914, 1925) and Stead (1932) noted polyandrous trios sharing the same nest, and sharing chick rearing among Brown Skua *Catharacta skua lonnbergi* on offshore islands.

The problem of a geographic mindset was clearly articulated by another New Zealand ornithologist, Richdale (1965), who stated:

"the phenomenon of three adult skuas at a nest, each one apparently equally devoted to the chicks, has usually caused skeptical comment whenever I have mentioned the fact in Northern Hemisphere circles".

In contrast, Richdale's studies of the more conventionally pairbreeding seabirds were readily quoted by Northern Hemisphere biologists (e.g. Lack 1954, 1966).

Communal breeding has been a feature of IOC meetings since 1974 (Frith & Calaby 1976) and it is hoped that the biases of geographic mindset are widening.

Theoretical influences

Communal breeding in birds was not considered of any special theoretical relevance until the mid 1960s. Most studies prior to this time were largely descriptive natural history, whereas now, many are at the forefront of behavioural ecology. More than 12 colour banding studies of communal breeding have been in progress for more than 10 years.

Behavioural ecology began with an amalgam of ideas from ethology, ecology and evolutionary theory (Barlow 1980, Silverberg 1980). The predominant emphasis is on a functional approach based on the assumption that natural selection acting on gene frequencies is the most important component of evolution (Brown 1987, Emlen 1984, Wilson 1975). The idea that life history patterns and reproductive behaviour can be adaptive responses to resource patterns and that this can be evaluated using costs and benefits came from ecology and ethology (e.g. Lack 1954, 1968; MacArthur 1962; Tinbergen et al. 1962). The environment was seen to impose problems that were solved by the action of natural selection on gene frequencies (see Gray 1988).

Hamilton (1963, 1964) provided an important extension to this when he proposed the idea of inclusive fitness via kin selection. The notion that an individual's genetic representation in subsequent generations could be enhanced by assisting relatives other than descendent kin provided the major impetus for communal breeding studies (see Brown 1978, 1987).

Subsequent developments of theory within behavioural ecology have built on these ideas but are still unified by the assumption that selection is universal. However, as Maynard Smith (1978) pointed out for optimality arguments, the involvement of selection is not under test, only how selection may potentially work. This seems to be forgotten by many workers (see Emlen et al. 1990). Paralleling the increased selective influence in behavioral ecology, there has been a questioning of such pan-selectionist approaches (see below). The latter development appears to have gone largely unnoticed in communal breeding studies, however.

The theories we use are very dependent on the ideas that prevail at the time. They lead us to ask specific questions, but it is important to include realistic alternatives or we may be left with only one possible answer. This does not mean that answer gives the best explanation, just that only one explanation was sought. In communal breeding, like many studies, straw alternatives have been used (see below) and have left the researchers with apparent support for their hypotheses.

We know theories influence what we look for, what we see and what we measure. Hence there are different ways of seeing (eg. Goodwin 1982) or different forms of blindness in biology. If Darwin, Lorenz, Wynne-Edwards, Hamilton and Jamieson had all viewed precopulatory behaviour in Pukeko all would have seen different things. Darwin may have seen from long chases how the male that is most attentive and chases the female longest obtains the copulation - ideas in accord with sexual selection. Lorenz would have been little interested in many birds attending a copulation but instead may have noted how similar the postures were to those of similar gallinules; Wynne-Edwards would have seen that some birds do not attempt to copulate supporting ideas of population restraint; Hamilton would have noticed that close relatives share copulation; while Jamieson would have noted that dominant males sometimes prevent and sometimes watch subordinates copulating. All are realistic interpretations of the observed behaviour, but each in isolation provides a limited description.

A major theme within biological theory, including communal breeding, stems from economics. Darwin was thought to be influenced by the free market ideas of Adam Smith (Schueber 1977). Optimality and game theory are derived from economic models (Axelrod & Hamilton 1981, Maynard Smith 1978, 1984) and allow biological accounting of calories, reproductive success, etc. Similarly, ideas of inclusive fitness encourage simple accounting whereby costs and benefits are evaluated in the currency of genes. While few biologists would argue that behaviours can be attributed solely to genes, genetic determinism has become a form of accepted shorthand for the idea that genes are involved (Dawkins 1982). For some, this equates with "bean bag" genetics (Haldane 1964). The approach has value but just as accounting (colloquial term is "bean counting") and economics provides only a partial understanding in commerce, so gene counting, or the counting of other currencies, will only form part of a holistic and multifactorial understanding in biology.

Study species and study area influences

No matter what theories we may wish to investigate or what variables we believe are important, what we end up measuring is greatly constrained by the nature of our study animal and its habitat. These pragmatic considerations also influence how we view the results from other communal breeding studies.

The social organization, behaviour and habitat of communally breeding birds varies greatly (see Brown 1978, 1987, Stacey & Koenig 1990). Some researchers must deal with birds that roam over large areas or live in forest and hence can only be seen at specific locations. Some (e.g. Emlen 1990) can observe multiple nests in a colony while others have to deal with widely dispersed nests (e.g. Koenig & Stacey 1990, Brown 1990). Moreover, determining which individuals are reproductive relies on observing copulations - a task of varying difficulty. For example, Rowley & Russell (1990) report seeing less than one copulation per year during a 17 year study. Koenig and Stacey (1990) average less than one copulation for every 50 hours specifically devoted to observing copulations. In contrast, it is not unusual to observe 10 copulations in an hour's watch of Pukeko groups (Craig & Jamieson 1990).

EXPLANATIONS OF COMMUNAL BREEDING

Given the extreme variability in the life history patterns, behaviour and habitat of communal breeding birds, it is surprising how similar are the explanations among the different studies. This apparent agreement probably derives from a common theoretical perspective in that most researchers (including myself) have adopted cost-benefit adaptive models (e.g. see Brown 1987, Emlen et al. 1990, Stacey & Koenig 1990 and references therein). Most agree that there are two major questions to communal breeding;

- (1) why do these birds live in groups rather than disperse and establish a breeding area as a pair? and
- (2) why do they help?

The answers to the first question have been derived from variable ideas of "habitat saturation" (Selander 1964, Brown 1969, 1974, Koenig & Pitelka 1981, Emlen 1982, 1984, Emlen & Vehrencamp 1983, Stacey & Ligon 1987). The major idea is that there is a limit to environmental resources necessary for breeding. For territorial species there is either a limit to total habitat, or more frequently, a limit to quality habitat. For colonial species, variability in food availability precludes all pairs from breeding each year.

Answers to why birds help raise the young of others, either by assisting in provisioning, or nest defence, are considerably more diverse (see Emlen 1984, Brown 1987, Stacey & Koenig 1990). Most workers have noted that the majority of helpers tend to be close relatives, especially young of previous years. Hence, from the ideas of the indirect component of inclusive fitness (Brown & Brown 1981), there is a potential genetic gain from helping behaviour. This answers the apparent paradox that helping is behaviourally parental but is genetically non-parental (Brown 1987). In addition, most workers note the potential for direct fitness benefits. These and other ideas are adequately detailed elsewhere (e.g. see Emlen 1984, Woolfenden & Fitzpatrick 1984, Brown 1978, 1987, Koenig & Mumme 1987, Stacey & Koenig 1990).

SPECIFIC ISSUES

What does kinship explain?

Numerous authors including myself (see Brown 1978, 1987, Emlen 1984, Stacey & Koenig 1990 & references therein) have argued that indirect fitness gains are a major

component of the explanation for the evolution of "helping" behaviour. However as Gould, Lewontin and others (eg. Gould 1978, Gould & Lewontin 1979, Lewontin 1983, Jamieson 1986, Gray 1987) have warned, the overwhelming appeal and apparent support of functional explanations may be misleading. While it is possible to count the average gene benefits of "helping" the costs are often measured in another currency. Without a common currency to measure costs and benefits, the interpretation becomes a value judgement. Too often the presence of apparent benefits is taken as support for an adaptive explanation. However, without realistic alternative models for comparison, the result is predetermined by the uncritical acceptance of theory.

Recently an alternative model that birds feed begging offspring purely as a result of a stimulus-response mechanism has been suggested (Jamieson 1986, 1989, Jamieson & Craig 1987, 1991, Woolfenden & Fitzpatrick 1990). Typically birds only encounter begging offspring when they breed themselves, but as a consequence of group living, communally living individuals may encounter the young of others. Such ideas can account for interspecific feeding and the feeding of parasitic young; behaviours that are problematical for pan-selectionist explanations.

The response of some researchers has been to argue that ideas of stimulus-response and indirect fitness represent different levels of analysis (eg. Emlen 1990). To these workers, a stimulus-response model may explain the origin of the behaviour, but indirect fitness components explain current selective maintenance. However, both indirect fitness and stimulus-response models can act as competing hypotheses and some workers have attempted to test one against the other (Emlen & Wrege 1988, Curry 1988, Clarke 1989). In all cases, tests that could be related to the stimulus-response model were formulated as an unlikely (straw) alternative to a selectionist model, and/or variables were confounded.

For example, Emlen & Wrege (1989) tested whether White-fronted Bee-eaters preferentially directed helping behaviour (provisioning of young) toward kin, as expected from indirect fitness concepts, or toward random nests. Given that no known behaviour is random, that birds defend nest holes against strangers and that birds only encounter the begging of young once they are in the nest hole, it is not surprising that the authors found a significant preference for kin. Curry (1988) considered the nearest nest within the same territory as a more realistic test for the stimulus-response model but failed to address the probability of a "helper" encountering the nearest nest. Clarke (1989) tested both the nearest nest and random nest models yet all three studies are confounded by familiarity. Even though Curry believed that familiarity explained the observed pattern of helping better than kinship, all authors subsumed familiarity as a cue for kinship. Given that familiarity with breeders is also expected to correlate with probability of encountering a begging stimulus, no realistic test of a stimulus-response model was undertaken and hence the model cannot be refuted.

Davies' studies of Dunnocks (Davies 1990 & references therein) provides some of the clearest evidence that the likelihood of paternity influences how male breeders apportion help at a nest. DNA fingerprinting showed that paternity correlated closely with the mate obtaining exclusive access to a female at the time when copulations occurred. Males only provisioned young in a nest if they had spent some exclusive time with the female. Such an all or nothing response is predicted from conventional theory (see Werram et al. 1980, Craig & Jamieson 1985). However, among β males, the

more time they had spent with the female the more likely they were to help. In other words, β males showed a graded response not the predicted theoretical response that males should help fully if there is any probability of paternity and should not help if there is no probability of paternity.

The alternative stimulus-response model and the potentially confounding variable of familiarity influencing access to the begging stimulus are not discussed, but appear involved. For example, where a male had two mates, he put all his effort into the nest with the most young and hence the strongest begging stimulus even though he was the father at both nests. In addition, males who lacked paternity or fathered a minority of offspring did so as a consequence of the α male denying them access to the female including while she was building the nest. Was it reduced access to and familiarity with the female and hence lack of access to the nest and the begging stimulus (as predicted by Jamieson & Craig 1987) or lack of paternity (as suggested by Davies 1990) that explains the level of feeding? Couldn't it be both? Surely future tests should incorporate both variables rather than assume a unifactorial explanation.

Familiarity, kinship and multivariate explanations

Do birds help kin or do they help familiar individuals? In human societies, because close kin (siblings, parents, offspring) are usually included with those with whom we are most familiar, there has been a temptation for researchers to assume that familiarity is the mechanism of kin recognition (e.g. Fletcher & Michener 1987, Emlen 1990, Curry 1988, Clarke 1989). If we accept tests of kinship theory that allow the most likely alternative behavioural mechanism - familiarity - to be dismissed as a fully dependent variable, is rejection of the theory possible? Subsuming familiarity means that support for alternative models, such as random association or attendance at the nearest nest regardless of whether the bird has had equivalent levels of association with the nest inhabitants, will be highly improbable. The result is apparent support for kinship theory solely because a realistic alternative was not investigated.

Why not consider familiarity as at least a partially independent variable? Many researchers argue for direct advantages of foraging in or establishing in familiar areas (e.g. Koenig & Stacey 1990, Stamps 1987, Brown 1987) and of breeding and interacting socially with familiar individuals (Sherman 1981, Fletcher & Michener 1987, Boonstra & Hogg 1988, Ferkin 1988, Yamamoto et al. 1989, Ylonen & Viitala 1990). Hence familiar associations can be beneficial irrespective of kinship.

Tests of kin recognition by preferential association with kin independent of familiarity have been done with many animal groups from mammals and birds to tadpoles and barnacle larvae (Holmes & Sherman 1983, Waldman 1982, Curry 1988, Bateson 1982, Fletcher & Michener 1987). These have shown that while many animals preferentially associate with familiar individuals there is an apparently stronger preference for kin. More recent experiments (Pfennig 1990) have questioned whether such results clearly demonstrate kin recognition. Pfennig suggests that attributes of a natal or familiar habitat are most important in determining association and that kin recognition may purely be a consequence of habitat choice.

For some people these arguments may seem unimportant. To them there is a potential for kin selection as long as "help" is more likely directed toward kin than non-kin (Dawkins 1982, Brown 1987). Rules of thumb for kin recognition, such as familiarity,

can achieve this and hence from a theoretical perspective the mechanism becomes unimportant, were the aims of our research solely to provide a full understanding of the behaviour of our study animals. From a theoretical perspective, observations that animals preferentially direct helping behaviour towards kin as a consequence of familiarity is supportive of the *potential* action of kin selection but is not a test of kin selection as many assume (see also Maynard Smith 1978 p35).

Most studies of communally breeding birds have shown a small proportion of individuals are not related to any others in their group (see Brown 1978, 1987, Emlen 1984, Stacey & Koenig 1990 and references therein). Familiarity may explain why they help whereas kinship cannot. Moreover, the use of molecular techniques is showing that among both communally breeding and other birds there is a variable level of extra-pair copulation and parasitic laying (Table 1). This will increase the levels of non-kin among family groups and may bring into question the degree of support for kinship models but will not alter predictions from familiarity models.

TABLE 1 – Frequency of extra-pair or extra-group copulations and parasite laying in birds.

Species	Extra-pair Copulations	Parasitic Laying	Source
Splendid Fairy-wrens	>65%	–	Brooker et al. 1989
White-fronted Bee-eaters	→ 9 - 12%	<–	Wrege and Emlen 1987
White Crowned Sparrows	34-38%	–	Sherman and Morton 1988
Indigo Buntings	27-42%	–	Westneat 1987
Eastern Kingbirds	30-53%	–	McKittrick 1990
Cliff Swallows	6%	24-43%	Brown and Brown 1988
Swallows (Denmark)	–	17%	Moller 1987
Pied and Collared Flycatchers	24%	–	Alatalo et al. 1984
Tree Swallows	24-32%	–	Morrill and Robertson 1990
Eastern Bluebirds	9%	–	Gowaty and Karlin 1984

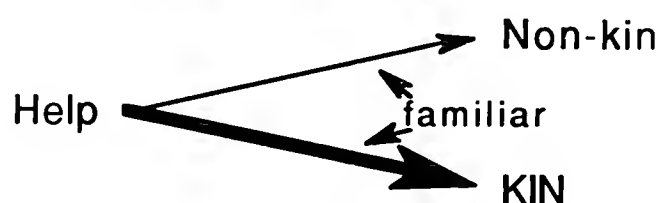
Even though it is not possible to separate familiarity and kinship in already published studies their results are highly supportive for familiarity being an important independent variable in addition to kinship. Wrege & Emlen (1987), Curry (1988), Clarke (1989), Davies (1990) and many other studies (see Stacey & Koenig 1990) found individuals helping familiar but unrelated individuals. The more familiar a “helping” individual is with the adults controlling a nest, the more likely it will encounter the nest and hence a begging stimulus. The consequence will be to feed. Curry (1988) and Curry and Grant (1990) even argue for the importance of familiarity but because they did not separate it from kinship they were left with no alternative but to preferentially reject the stimulus-response model.

Future studies should acknowledge the likely importance of both kinship and familiarity in determining associations among individuals. Combining observation of behaviour with molecular tests of parentage to determine kinship, and measuring familiarity by frequency of close association will allow more realistic tests of existing models and their interdependence (Figure 1).

Kin mating and incest avoidance

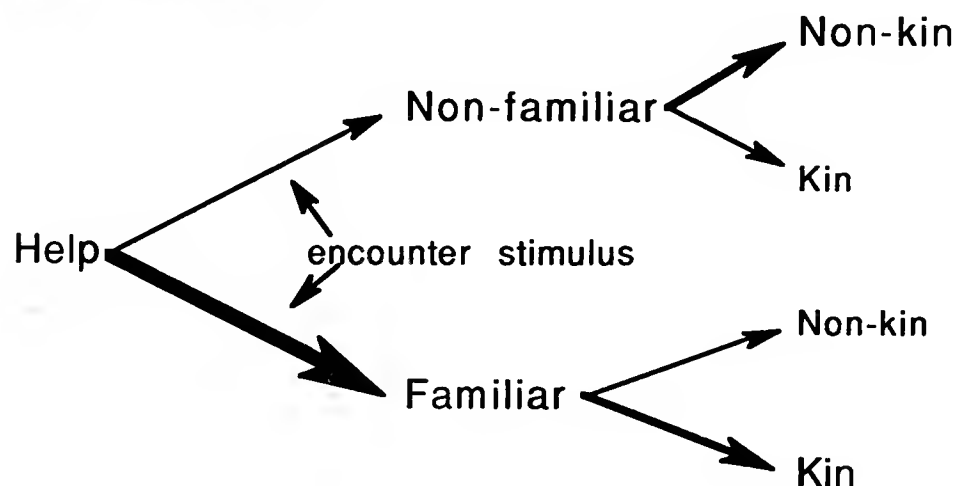
Kin groupings so commonly found in communally breeding birds provide ideal situations for evaluating ideas of inbreeding avoidance. In spite of the theoretical notion that inbreeding is but one extreme of a continuum of mating with outbreeding the other extreme (e.g. Shields 1982), most workers treat inbreeding in isolation. Inbreeding can be potentially disadvantageous in a normally outbreeding population but it is often forgotten that outbreeding can be equally problematic in typically inbred populations (Craig & Jamieson 1988).

Inclusive Fitness model



univariate model

Stimulus-Response



multivariate model

FIGURE 1 - The relationship between kinship and familiarity in expression of helping behaviour. a) Inclusive fitness model that subsumes familiarity as the recognition mechanism for kinship. This model has current acceptance. b) Stimulus-response model that assumes that the degree of association individuals have will determine familiarity and hence the likelihood of encountering a begging stimulus. Kinship may or may not add additional explanatory power.

Few workers have attempted to consider the full range of variables. Whether individuals mate with relatives is affected by a number of issues including incest avoidance, dominance, reproductive competition and mate choice. Reproductive competition by intra-sexual dominance can either be by fathers or replacement males dominating and preventing helpers (sons) from copulating with their mate (the helpers mother) or by a group of outsiders displacing a smaller number of existing male residents (e.g. Acorn Woodpeckers - Koenig & Pitelka 1979, Hannon et al. 1985). Dominance may be so extreme that individuals are psychologically castrated (Reyer et al. 1986) and hence appear incapable of responding sexually or aggressively in the short term. Inter-sexual dominance may explain why a female will not copulate with her son but would rarely apply to fathers avoiding mating with daughters. In addition some females may not choose to mate with young males because of reproductive inexperience. A number of bird studies have shown that females with young males have lower

reproductive success than those with older males and that females prefer older partners (see Bateson 1983, Walters 1990). However, Walters (1990) suggests that even though young males make poor reproductive partners in Red-cockaded Woodpeckers the movement of the female away from her sons relates to incest avoidance.

Many recent reports of communal breeders still suggest the likelihood of incest avoidance (Brooker et al. 1990, Zahavi 1990, Koenig & Stacey 1990, Ligon & Ligon 1990, Rabenold 1990, Woolfenden & Fitzpatrick 1990) and some even assign attributes such as reduced hatchability of eggs to inbreeding depression (Ligon & Ligon 1990). With the exception of the work on Acorn Woodpeckers (Shields 1987, Craig & Jamieson 1988, Koenig & Stacey 1990) none have tried to systematically test alternatives.

Some workers argue that dispersal of one sex further than the other is a form of incest avoidance (e.g. Zahavi 1990, Rabenold 1990, Walters 1990). A contrasting view is that reproductive competition (both inter- and intra-sexual) will ensure dispersal and that the consequence of this may be a reduced probability of incestuous mating. As Ligon & Ligon (1990) found dispersal can still allow incestuous mating to be common.

Realistic evaluation of incest avoidance should contrast all explanations of observed mating patterns and where possible attempt estimates of the frequency that close relatives of equal status are available at the same time and the same place for mating. This can then be compared with observed levels. The observation that few or no incestuous matings are seen is poor evidence for incest avoidance behaviours.

TABLE 2 – Incestuous mating among communally breeding birds.

Species	% Incestuous mating	N	Source
Pukeko	>70%	107	Craig & Jamieson 1988
Splendid Fairy Wren	27%	270	Rowley et al. 1986
	9%		Brooker et al. 1990
Galapagos Mockingbirds	7%	156	Curry & Grant 1990
Groove-billed Anis	1.6%	127	Koford et al. 1990

Some communal breeding studies report relatively high levels of incestuous mating (Table 2). Many studies suggest that levels of inbreeding between 1-3 % are of little consequence among typically outbreeding animals (e.g. Soule 1983, Shields 1982). Where levels of inbreeding regularly exceed 3%, inbreeding may be considered part of the mating system and hence it is unlikely that deleterious effects of inbreeding will be detectable.

Rowley et al. (1986) reported high levels of incestuous mating but no significant difference in reproductive success of inbred versus outbred pairings. However, the overwhelming scientific belief in the deleterious effects of inbreeding led Rowley to conclude that his results were anomalous. DNA fingerprinting has shown that at least 65% of young do not belong to the male in the territory. The results allowed the researchers to return Splendid Fairy-Wrens to theoretical normality by suggesting they may have an inbreeding avoidance mechanism in promiscuity! Recalculated incest levels are still well above most species at around 9% but were conveniently not calculated.

These results of high levels of extra pair copulations greatly reduce the level of relatedness between helpers and the young they feed. As Rowley & Russell (1990) state, this will markedly lessen indirect fitness gains. Many individuals, thought to be feeding relatives are provisioning non-relatives. Follow up of future relationships will allow an interesting test of whether kinship or familiarity better explains helper associations and mating patterns.

SUMMARY AND CONCLUSIONS

Science is influenced by changing fashions in theory as well as local and regional biases. For example, studies of communally breeding birds have increased greatly since the advent of theoretical ideas such as kin selection and inclusive fitness (see Brown 1987). Prior to 1970 most studies were largely on aspects of natural history. Acceptance of the communal breeding phenomenon appears to have been far more rapid among Southern Hemisphere ornithologists. The high frequency of pair breeding birds that hold breeding territories only seasonally in the Northern Hemisphere led to skepticism toward the phenomenon among researchers from that part of the world.

Similar biases due to theory and our own encounters with nature greatly influence the questions we ask and the conclusions we reach. Even though there has been increased questioning of adaptive or selectionist reasoning since the late 1970s (e.g. Gould 1978, Gould & Lewontin 1979) this debate is only just impacting on studies of communal breeding (e.g. Jamieson 1986, 1989, Jamieson & Craig 1987, 1990, Emlen et al. 1990, Ligon & Stacey 1989, Mumme 1991). Initial responses to the plea to include realistic evaluation of many alternatives including nonselectionist models have been confusing (e.g. Curry 1988, Clarke 1989, Jamieson & Craig 1991). A major problem has been the subsuming of important variables such as familiarity as a mechanism for the theoretically important kin recognition. This assumption has meant that attempts to formulate models from stimulus-response ideas have largely produced straw alternatives that have been easily dismissed.

Other examples of investigation where workers appear driven by conventional interpretation of theory include the idea of incest avoidance. In all examples, workers are urged to expand the range of questions asked to include the four questions suggested by Tinbergen (1963): causation, development, function and evolution. There is a need to increase our efforts at identifying more of the likely variables that influence the behaviour of communally breeding birds and how these variables interact. Future studies need to be multifactorial and be aimed more at describing, understanding and predicting the birds' behaviours rather than simply supporting the conventional readings of theory.

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PLENARY LECTURE

**APPLIED ORNITHOLOGY:
PUTTING THEORY AND PRACTICE TOGETHER**

E. H. BUCHER

APPLIED ORNITHOLOGY: PUTTING THEORY AND PRACTICE TOGETHER

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Man as a biological species has opted for manipulating the environment instead of passively adapting to its vagaries and restrictions. As a result of that, we have enough energy, resources, and time available to allow ourselves to get involved in many activities besides our basic biological duties, including science. During this century, scientific research has become a widespread, full-time professional activity, which in turn has contributed to increase our ability to manipulate the external world still further. Consequently, scientists are expected to be able to solve nearly all kind of practical problems, including those caused to the environment precisely by our ever increasing technological capabilities.

Having played a crucial role in alerting the world on the risks of forest destruction and biodiversity loss, ornithology is certainly well involved in the applied-versus-pure research conflict. Ornithologists are permanently requested to be relevant to society, and the IOC parallel meetings organized by the International Council for Bird Preservation have been alerting us for several years on the magnitude and difficulties of the problem of protecting birds from extinction. The decision of including this topic in an IOC meeting is a clear indication of the ornithologists' growing concern regarding their duties and responsibilities in society.

Indeed, the science of ornithology has an outstanding record of contributions to the solution of applied problems. Many of the basic concepts firmly established in management today were first coined within ornithology, some of them after longstanding, vigorous theoretical arguments. Emphasis in applied ornithology has shifted throughout the years from gamebird hunting and birds as agricultural pests to species conservation, and the preservation of biodiversity. Well established principles originally derived from studies of birds include:

- a) The existence of density-dependent mechanisms of population regulation, and their counter-intuitive connotations for management. This may preclude achieving increased harvests via predator control in game species, and make massive killing an unsuccessful method of pest control (Murton 1971).
- b) The existence of a critical minimal size below which a population is susceptible to extinction due to behavioural, genetic, and stochastic factors.
- c) The importance of behavioural aspects in bird management, including captive propagation and reintroduction of bird species to the wild.
- d) The existence of a complex correlation between habitat structure at different dimensions and scales, and species survival, which has important implications for the design of reserves.
- e) The existence of areas of high diversity ("hot spots") which deserve special conservation efforts.
- f) The importance of some bird species for pollinating flowers and dispersing seeds.

There are numerous examples of successful applied research projects in ornithology throughout the world, too many to enumerate here. Several of them have been carried out by New Zealand ornithologists. New Zealand's conservation research includes fine examples of well designed and well implemented projects that have saved local species from extinction by means of intelligent and innovative manipulations (Napper 1989, Bell 1991).

A growing concern

Despite the outstanding record of contributions made by ornithology and other environmental sciences to management, there is a growing feeling among the public, politicians, decision makers, and funding agencies that not enough effort and expertise is being dedicated by academic sectors to the solution of environmental problems at this time, when the future and fate of our planet is at risk.

In fact, we all face, to a varying degree, a moral and practical dilemma between pursuing our own "pure" interests in science or concentrating on the solution of problems, some of them of enormous magnitude, such as the effects of global changes in climate or the massive extinction of species. These conflicting feelings are currently being debated in nearly all academic circles dedicated to environmental sciences. Discussions usually include points such as whether we can afford to continue to be involved in "hobby projects" (as called by the utilitarians) that might lead to the discovery of another subtle ecological process in the tropics, instead of concentrating all our efforts on crucial problems such as saving the tropical rainforests from total destruction. Unfortunately, long debates often lead only to more debates without practical results. Even more frequently, empiricists, theoreticians, and "applied" scientists seem to have become increasingly isolated and entrenched in their own intellectual positions allowing little room for effective collaboration.

Another aspect of the same moral dilemma has to do with a growing availability of funds for applied research that has led some scientists to proclaim interest in applied problems as a way of obtaining extra funding, without a real commitment to solving them. As a result, it is not unusual that funds targeted for the solution of specific problems may in practice be used to carry out research that is irrelevant to the final goal. Moreover, in many cases priorities set for applied research programs often reflect the personal interests and perceptions of the members of the board rather than the real needs. Although reasons for such a strategy in a competitive world of constantly changing priorities are evident, it cannot be justified on both ethical and practical grounds. I am convinced that improper targeting of funds intended for applied research is greatly reducing the effectiveness of the available resources throughout the world.

Indeed, the whole issue of applied versus pure research is a moral one. Clearly, if we are studying birds that live in the real world, we must be prepared to help to manage that world as efficiently as possible. It is also very clear that management decisions need to be taken within short time, and that pressures and vested interest are always present. We can then expect that decisions will be taken anyhow, and without the best possible advice, unless scientists endeavour to find better alternatives and are determined to advocate in favour of them in an effective and articulate way (Williams 1990).

Despite its obvious relevance, I do not intend to insist here on the moral aspect of the applied versus pure research dilemma, for two reasons. In the first place, I feel that

awareness and moral issues in the environmental sciences were critical a couple of decades ago but have already been widely discussed. Today, the academic community is already well aware of the implications. Second, I firmly believe that other crucial aspects of the problem, particularly those related with the implementation of applied science, are equally critical and deserve consideration. In other words, I do not feel that we will solve our growing environmental crisis by simply demanding every ornithologist to become permanently involved in practical problems, particularly when by doing so they may be forced to divert from the fundamental basic questions in which they have deep interest and expertise. On the contrary, priority should be given to find practical ways of making useful contributions to problem-solving without losing the motivation and the productivity that each one of us has when pursuing the fundamental questions and the inquisitive awe which first led us to ornithology.

Furthermore, I would like to discuss alternatives that may enable us to make the most from the intellectual polymorphism currently in the scientific community. We need to promote a positive feedback between the search for general principles in science and the efforts aimed at solving specific problems. In other words, I argue that the fundamental challenge we face today is for us to perceive the need for an improvement in our traditional approach to applied problems, and endeavour to implement them as fast as possible.

In order to analyze that possibility, I would like to discuss the following points:

- a) What are the problems that interfere in the interaction between pure and applied research?
- b) Are there better alternatives for implementing applied research in ornithology and related environmental sciences?.

Problems in developing applied research

From my own experience, there are some identifiable factors in the present academic world that conspire against a better interaction between the academic and management sectors. Some of these problems are deeply rooted in human behaviour. The following deserve special consideration:

UNIVERSALITY VERSUS PRACTICALITY: In academic circles applied research tends to be considered both less attractive and less prestigious. Such feelings are rooted in their perception of science as a discipline aiming at the discovery of basic laws and principles that govern the universe. In Einstein's words, "science is a search for those highly universal laws...from which a picture of the world can be obtained by pure deduction" (Popper 1965). Accordingly, theory-minded ornithologists are sometimes reluctant to become involved in what they consider economically useful but intellectually trivial investigations. As a result, many theories are never tested in practice due to the lack of interaction between "theoreticians" and "empiricists" (see Roughgarden et al. 1989). Furthermore, according to Slobodkin (1988) "Ecology in the absence of practical questions is in danger of deluding itself by a vain hunt of generality, answering only easy questions that it poses for itself, and becoming irrelevant to anyone outside its own academic village."

On the other side, ornithologists involved in applied problems may lack exposure to the present-day status of the art in theoretical ecology. Consequently, applied scientists may miss the opportunity to gain access to a wider conceptual framework that

may provide them with new techniques and perspectives of great practical value. Lack of interaction between theory and practice may also make applied scientists unable to take advantage of management practices (such as predator control, prescribed burning, etc.) as large scale experiments where theories can be tested. Consequently, practical questions in environmental management in the absence of sound ecology are likely to receive misleading and even dangerous answers.

INCREASING SPECIALIZATION: a growing tendency to specialize does not favour selection for a holistic approach to science. In any specialty, the need of keeping pace with a discipline tends to preclude investments in widening field experience and the awareness of developments in other areas, not to mention seeking ways for making the specialist's work useful. Ecology was once considered a truly "holistic" science, but to a large extent is losing its conceptual unity.

Although specialization is absolutely essential in science, given the exponential increase in the body of knowledge and a growing competition between scientists, it should not mean a drastic (and debilitating) narrowing of a scientists' interests. Unfortunately, this is not usually the case. As a consequence, scientists capable of keeping a holistic approach when dealing with applied problems are increasingly rare. In fact, there are growing pressures to specialize, in order to be successful, but at the same time the questions we ask increasingly require broad, synthetic answers.

FASHIONS: research fashions change periodically, often without having completely solved the initial challenge. So do the search for suitable species and field conditions that may favour testing the presently discussed hypothesis.

Although fashions have proved to be very important in promoting an accelerated development of specific areas of science, they can also have the negative effect of discouraging at least momentarily other areas that are equally important or necessary. Examples include the "shading out" of population ecology during the community ecology era, and the lack of support for projects of sustainable management during the "reserve-oriented" times in conservation.

Preference for fashionable themes and disdain for research relevant to the local reality is sometimes an unwanted result of postgraduate training of students from underdeveloped countries in centers of high academic excellence in the developed world. The problem may be designated as "type 2 brain drainage", type 1 being the actual emigration from the country.

TERRITORIALITY: Although man is a relatively gregarious species, cooperation is not always easy, particularly within the academic environment. Communication and collaboration is difficult between individuals, departments, institutions, and disciplines. The widespread "lonely wolf" attitude corresponds well with the average scientist's inclination for independence and personal control of his or her environment.

Lack of communication and interaction between disciplines is also widespread. The following quotation exemplifies a common situation: "A quantum leap in progress could be made if evolutionary and population biologists mellowed in their widespread animosity for ecosystem science" (Schlesinger 1989).

Isolation is commonplace between government agencies and research centers, despite the obvious need for collaboration between both. Researchers at government agencies can very rarely carry on in-depth research on the large variety of problems they have to face. At the same time, universities tend to lose contact with reality unless they are connected with those applied biologists on the "front line." Full-time and full-life careers in the university that do not expose scientists to the "real world," may lack the formative input and motivation that even short periods in government or private agencies may provide.

LACK OF INSTITUTIONAL EXPERTISE IN INTER-DISCIPLINARY RESEARCH: Institutional programs aimed at the solution of applied problems are usually managed in exactly the same way as any other scientific program, ignoring their unique needs for the implementation and coordination of inter-disciplinary research. As a result, a substantial proportion of the budget may go to scientifically sound but irrelevant research, key components of the problem may remain undetected, no effective interaction between managers and extensionists develops, and findings remain unnoticed by the potential users.

Short-term funding also poses another problem that may seriously impair applied programs which generally require more than one fiscal year to attain meaningful results.

MISCONCEPTIONS ABOUT APPLIED SCIENCE: Several pervasive "myths" about applied science tend either to make people reluctant to become involved in applied work or lower the success of applied research programs. The more noticeable misconceptions include:

- 1) Applied research is always intellectually unchallenging and trivial.
- 2) Any good scientific study contributes to better management.
- 3) Comprehensive surveys and descriptions are the necessary first step.
- 4) Each new problem is unique. There are few background principles, information, or even comparable past cases.
- 5) Management, implementation, evaluation, monitoring, and extension is for someone else, somewhere else.

Such misunderstandings are largely the consequence of approaching applied problems with the same point of view and methodologies used in basic research.

The alternatives

I believe that the goal of solving applied problems in environmental sciences implies not only commitment, but also the need for the application of adequate concepts, procedures, and techniques. Although we scientists are well aware of the importance of sound methodologies and experimental design in our own research, we tend to disregard the need for appropriate techniques in implementing applied projects, feeling that this is something that anybody can do just by inspiration, which usually is not the case. At the same time, the need for more efficient methodologies should not lead us to forget that techniques alone are not enough. The best of techniques, unless guided by a clear vision of the fundamental issues and by a concept that gives them form, can turn solutions into larger problems.

Improving our approach to problem solving requires at least a) finding creative ways of facilitating interaction between theoreticians, empiricists, and managers, and b) providing them with the intellectual and logistic framework necessary for interaction.

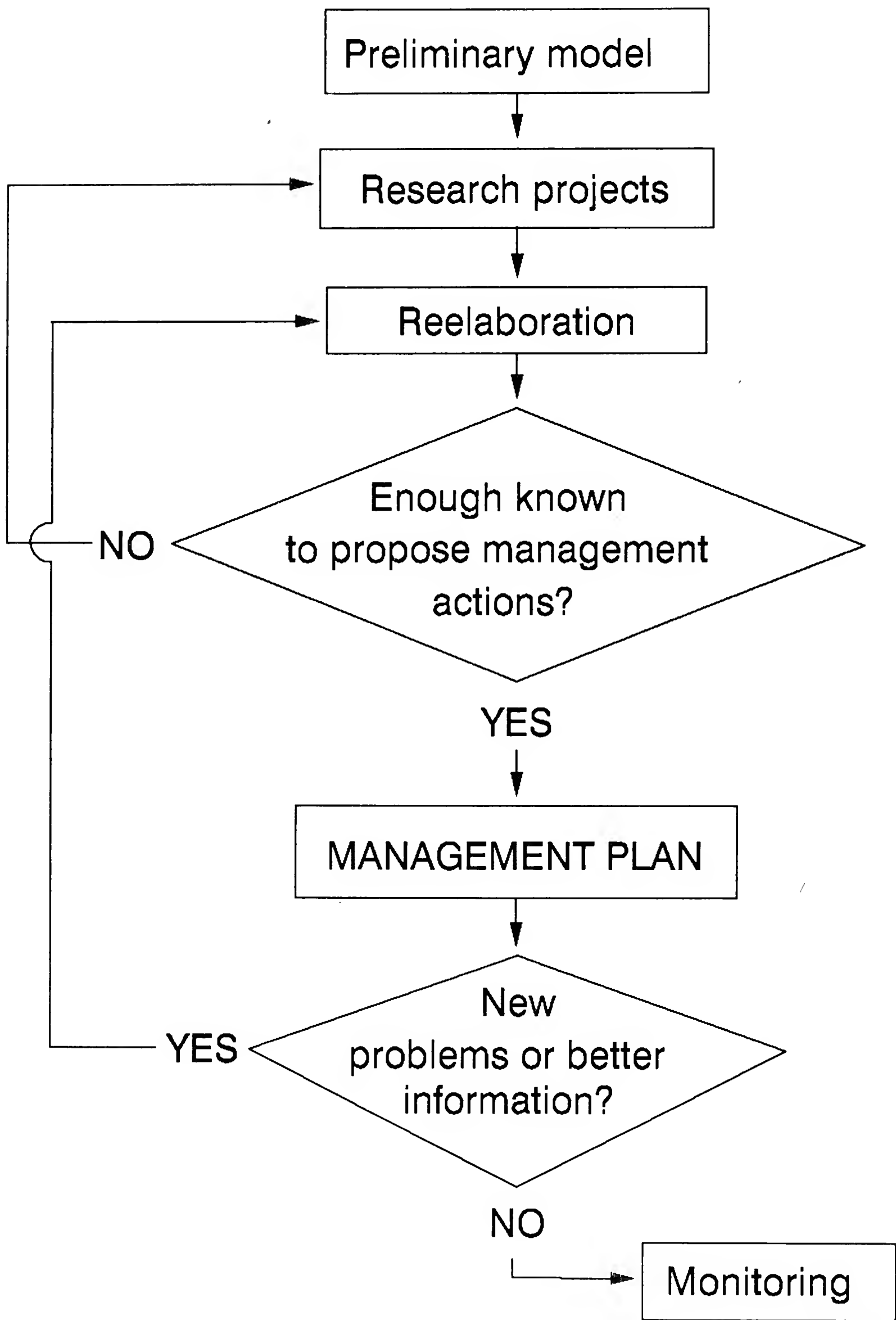


FIGURE 1 – Basic steps in the development of a “strategic” management program.

One possible way of achieving that goal is to replace the traditional, discipline-oriented style of research by a goal oriented approach, in which all research is subordinated to the management goal in a systematic, interdisciplinary way.

Such a "strategic" approach is not new in other areas of science and technology, including business, industry, and military science, usually associated with operational research. Moreover, Holling (1971) has already demonstrated that many sophisticated techniques developed in systems sciences (like optimization methods and decision theory) can be usefully incorporated in environmental impact assessment. However, it has not been widely adopted in ornithology or in the ecological sciences in general. Reasons for that include the problems and constraints already discussed, as well as the fact that these ideas are usually presented in a complex mathematical language, which is less accessible to non mathematic-minded naturalists.

In simple terms, a strategic approach consists essentially of the following steps (Figure 1):

- a) Definition of the management goal.
- b) Elaboration of an initial model based on available information.
- c) Detection of research priorities and needs in terms of the management goal, and elaboration of the respective research projects.
- d) Re-elaboration of the original model based on the information obtained from the first round of research projects, iteration of the whole process if necessary, and elaboration of management recommendations.
- e) Monitoring and readaptation if required.

As such, a strategic approach does not rely on a once-forever set of recommendations of predictions, but rather provides a flexible, interactive approach to management needs. And we must accept that uncertainty is an inevitable component of the behaviour of all complex systems (Holling 1978, Ehrlich 1989).

A strategic approach to applied science has several advantages over the traditional basic approach. First, the goal determines the priorities. A strategic approach ensures that all the relevant components and driving forces of the problem are considered in an interactive way, instead of allowing useless competition for the available resources among disciplines. This also avoids the selection of only those aspects that are intellectually fascinating as well as technically feasible, and the rejection of those aspects that are less fascinating or less feasible but equally important in terms of the final goal. In the second place, by proceeding in an interactive way, the program can be permanently evaluated, improved, and redirected if necessary. A constant process of re-elaboration of the original model can provide decision makers with the best available advice whenever necessary, instead of postponing any recommendation until the final report. This is particularly important given that management problems generally require assessment and corrective action long before comprehensive models can be constructed. On critical issues, where only quantitative assessments are needed by policy makers, the strategic approach may prove to be extremely useful even in its early stages of development. Finally, a goal-oriented project is easier to be evaluated, improved, and redirected if necessary. By promoting only goal oriented research it also helps to maximize the benefit to cost ratio of the investment.

Under this basic structure, the process of research can be expanded and refined by using all available methodologies. Each subset of the problem can be reanalyzed

following the same procedure, until the single-project level of detail is reached. Mathematical modelling and other techniques can be included to better understand specific sectors or interactions. At this point, an ideal stage is set for facilitating interaction between theoreticians, empiricists, and managers regarding specific sub-problems within the project.

Implementation of a strategic approach to research requires the interaction of specialists under a coordination capable of keeping the whole process without deviating from its original course. In its basic form, the whole project can be conducted through a series of workshops (Holling 1978), although other mechanisms may be equally practical, providing that the basic steps and goals are maintained. In practice, however, implementation of a strategic approach to research is not without difficulties, and several problems can be expected at the researcher, institution, and funding agency level.

Coordination is critical. The role of the coordinator is a complex one, that requires not only scientific but also managerial skills. Lack of clear leadership or clear operational rules (authorship, etc.) may prove fatal to any project. Unfortunately, training for such a role is not usually included in university programs in natural or environmental sciences. Other potential problems include the lack of specialists, lack of motivated people, and personal conflicts (territorialism, "prima donnas", politics, etc.).

Goal-oriented research has two basic forms of implementation at the institution level. One is to concentrate all researchers in one institution devoted to solving a specific problem or a group of related problems (the "institutional" approach). The other possibility is to set up temporary teams integrated by scientists of different institutions to deal with specific problems (the "horizontal" approach). Expected problems of the institutional approach include a lack of flexibility, ageing and overgrowth.

Researchers may sometimes feel frustrated by the need to deal in a superficial way with a succession of problems without having the chance of deepening their skills and knowledge in one specific subject, and therefore become reluctant to keep pace with new needs and challenges. Moreover, in some cases problems appear and disappear at a much faster scale than originally expected, creating the need for sudden shifts in priorities. Finally, it is also possible that an institution will become dependent on the continued existence of the problem for its own justification and survival, which obviously conflicts with its ultimate goal.

The "horizontal" approach is well established in the industry and business sector, but is uncommon in the academic arena, where strong individualism is widespread. Even when research teams are implemented, there is usually a confusion between fully interactive, goal oriented, "interdisciplinary" teams, and "multidisciplinary" groups where members work on different aspects of the problem but in an unrelated way.

Although difficult to implement, a strategic approach to research is by no means impossible, and certainly is one of the few practical alternatives potentially capable of providing the adequate framework for effective interaction between ornithology and other environmental sciences, and critical present applied research needs. Moreover, it may well help us to take the lead in stimulating interaction with other disciplines of crucial relevance to environmental issues. In the words of Ehrlich (1989), "Here, as

in virtually all aspects of the application of the theory of population biology for the benefit of the humanity, we must either gain the cooperation of social scientists or invade their turf. The former is infinitely preferable, for obvious reasons.”

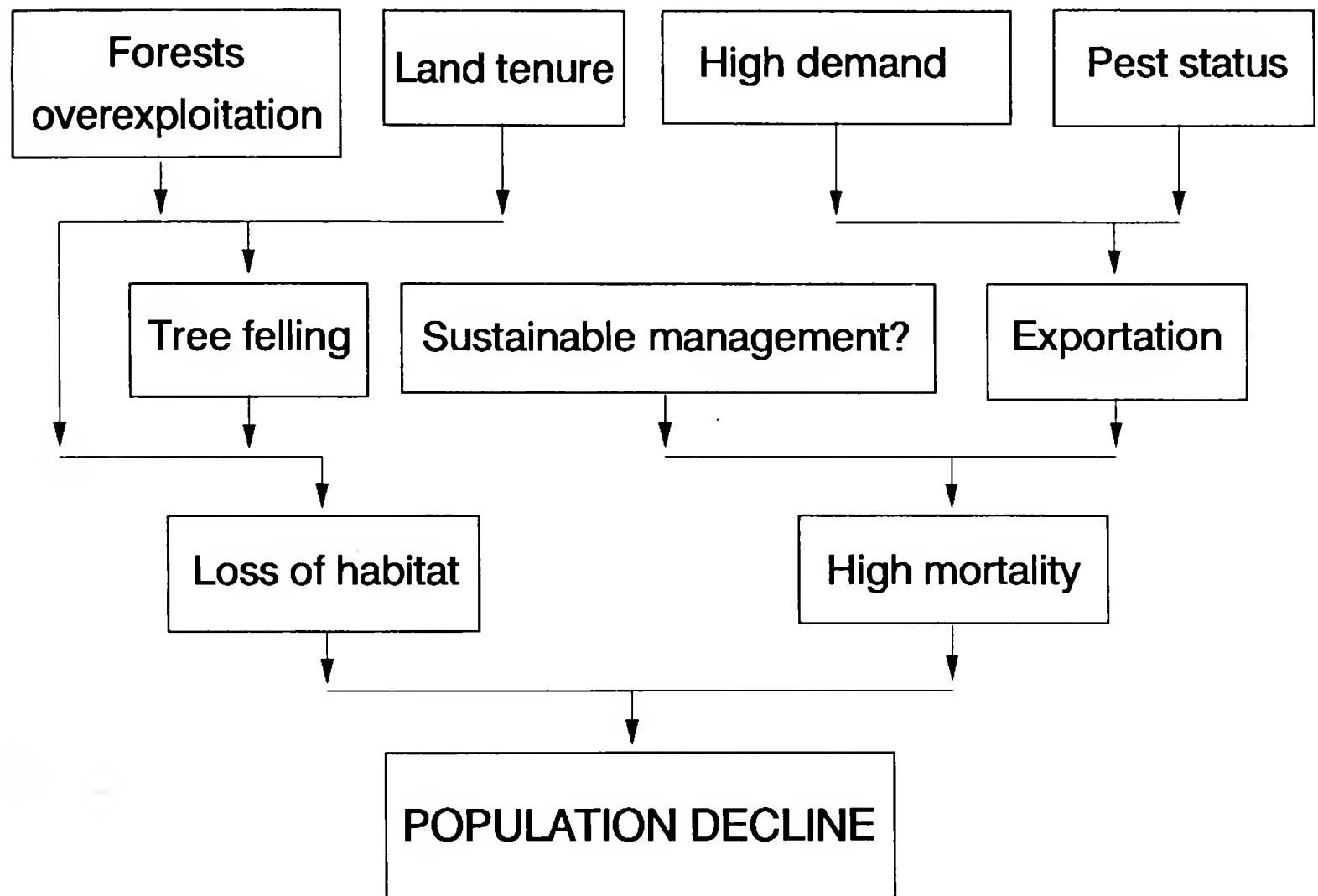


FIGURE 2 – Main factors influencing the present decline of the Blue-fronted Amazon in Argentina (see Beissinger & Bucher in press, Bucher in press).

Finally, isolated scientists can also benefit from adopting a comprehensive, goal oriented approach in their applied research projects. By keeping a wide interest and awareness on the whole system within which their own problem is included, they can gain a much better perspective of how their own subject is related to other interacting factors.

In summary, by following a strategic approach to applied problems, research can be conducted in a more productive way, better questions can be asked, and more interaction elicited between disciplines. The use of a strategic approach does not dismiss the value of other kinds of research approaches on the subject. Even if only laterally related to the problem, all research has the potential for making an important contribution to our understanding of the system, or even to result in an unexpected breakthrough that allows a better way of solving the problem. However, when resources are limiting (as they nearly always are), prioritation and optimization of research efforts becomes an unavoidable necessity.

The case of the Blue-fronted Amazon in Argentina

As an example of the complexities and implications of using a strategic approach in ornithology, I will briefly discuss the problem of exploitation of the Blue-fronted Amazon *Amazona aestiva* in Argentina.

This species was abundant in the Chaco savannas of Argentina until the beginning of the 1980s, when intensive trapping began as a result of a booming demand for the pet trade. Exportation of parrots from Argentina was declared legal and unrestricted due to the pest status that Argentine authorities assigned to almost all parrot species. As a consequence, about 204,000 Blue-fronted Amazons were exported from Argentina between 1981 and 1987 (Traffic Uruguay, unpublished report).

Although accurate figures are not available, there is circumstantial evidence indicating that in fact the population is being rapidly reduced both in numbers and in range (Bucher et al. unpublished report to the World Wildlife Fund). The potential for the species becoming endangered has been under close scrutiny by international conservation organizations, and the World Wildlife Fund has sponsored a research program aimed at verifying the sustainability of such intense exploitation.

The strategic approach already described shows the following to be the main factors influencing the present decline of the Blue fronted Amazon in Argentina (Figure 2) (Beissinger & Bucher in press, Bucher in press):

- a) Strong demand: Parrots have become fashionable pets in Europe and the United States. As a result, a sustained demand and associated high prices transformed the parrot trade to a very profitable business. The trade chain extends from the campesino in the Chaco, where each fledgling sells for about US \$7, to the pet stores in developed countries, where each Amazon sells for around \$400.
- b) The legal pest status assigned by Argentinean authorities to the species allows for unlimited export quotas from Argentina.
- c) Severe nesting habitat destruction is caused by local campesinos who destroy the nesting cavity or even cut the tree in order to gain easy access to the nestlings.
- d) Land tenure problems on both public and private land facilitate unrestricted exploitation of wildlife in the Chaco savannas, as well as the destruction of good tree habitat for parrots.
- e) There is a lack of expertise to implement sustainable exploitation schemes (ranching) which could offer a viable alternative to the present irrational exploitation.
- f) Superimposed on the problem of parrot overexploitation is a continuing process of forest cutting in the area. This poses a serious long-term threat to the survival of the species in the region. Forest cutting averages about 300,000 ha/year affecting mostly mature forest, a preferred breeding habitat for Amazons. The combined action of these factors is simultaneously causing important breeding habitat losses to parrots and high mortality. These factors are the most likely causes of the observed decline. From the analysis of Figure 2, it becomes clear that in order to stop the present population decline, all factors require simultaneous consideration. Unless all of them are managed properly, advances in only some of them will probably not help to achieve the ultimate goal. For example, even if a total export ban is dictated, high international demand will continue to exert a pressure that may be solved via sustainable ranching or diverted into poaching and smuggling. Unsolved land use problems may also prevent otherwise well designed sustainable ranching programs from being successful. Furthermore, unless the problem of deforestation and land use are considered, long-term survival of the species will continue to be threatened. In order to optimize efforts and resources, each of the detected factors can in turn be rated according to its importance in terms of achieving the final goal, and also the kind of action it requires be considered.

Actions may include not only research, but also education, legal enforcement, regional development planning, etc. Although in many cases those actions are not within the capabilities and commitments of a research team, adequate dissemination and transfer of the findings to the interested sectors may result in an important contribution to the achievement of the final goal.

Once the preliminary model has been obtained, and all the known main driving forces and key factors identified, each one can in turn be analyzed following the same procedure, until each factor becomes equivalent to a research project. For example, a lack of know-how of sustainable management can in turn be subdivided into several interacting components. When this stage in the process is reached, the need for modelling and utilization of already existing experience becomes clear. By keeping each research project within the context of the matrix, it is much easier to delineate and conduct each one of the research projects in an interactive way. For example, parrot population models, vegetation regeneration models, and international demand estimates need to be highly interactive in order to estimate exportation quotas or production costs in a given year. Moreover, a careful analysis of experiences from similar situations in equivalent species or equivalent ecosystems may provide significant clues and allow at least preliminary approximations during the first stages of the project.

The whole process can be iterated as long as necessary, not only for the initial phases of the management program, but also during its implementation in order to respond in a flexible and adaptive way to unexpected outcomes.

Management recommendations can be produced at any moment during the process, which hopefully will become more and more refined and specific with time. For example, the preliminary assessment clearly indicates that a total ban on trade should be imposed immediately in order to stop a rapid process of habitat deterioration and exploitation, and the reopening of the market should be considered only after sufficient experience on sustainable management has accumulated. At the same time, research should be initiated on agricultural damage evaluation and non-lethal ways of controlling bird damage. Finally, information transfer to the sectors involved in forest management and conservation is urgently required in order to deal with the long-term deforestation problem.

A traditional approach to the same problem risks overemphasizing a few aspects of high academic interest or those that are easier to observe (probably within the biological side), and may tend to ignore others that are more difficult or less interesting to analyze but equally important in terms of the final goal (such as migration, food availability, or land tenure problems).

Concluding remarks

- 1) Applied research in ornithology has already made important contributions to management. However, the present needs require increased efforts from ornithologists to solve our dramatic environmental crisis.
- 2) Ornithologists should not allow specialization to narrow their interests to the point that they lose the possibility of interacting with the real world where the birds live.
- 3) Involvement in applied problems by ornithologists requires not only commitment but also adequate approaches and techniques. Applied research programs would

benefit from developing a strategic, interactive, goal oriented approach, both at the individual and (ideally) at the inter-disciplinary team level. However, it should not lead us to forget that techniques alone are not enough. The best of techniques, unless guided by a clear vision of the fundamental issues and by a concept that gives them form, can turn solutions into larger problems.

- 4) Interdisciplinary, interactive, goal oriented research requires changes of attitudes and policies of individuals, research institutions, and funding organizations, which may prove difficult to implement, although not impossible. However, neglecting the need to make applied environmental research more efficient in a rapidly changing world may have serious costs in misspent resources and lost opportunities.

A final comment

There is no doubt that the world is heading into more, greater, and perhaps unexpected environmental problems. It is also clear that time is running out, since we are involved in processes that behave in an exponential fashion. We need new attitudes, more skills, and more commitment if we expect to deal with these problems with some success. We also need to play a more active role to force the real world to incorporate systematic and objective analysis of environmental sciences. Certainly this is not an easy task. Coming from the neotropics, where the conservation battle is being rapidly lost, I cannot be very optimistic. However, we do not have many options left. Otherwise, we ornithologists will have to satisfy ourselves with providing detailed and useless descriptions of the causes of extinction of an increasing number of bird species.

There is some room for hope if we remember that ornithologists have already shown their ability to provide important insight and influence in helping the world to become aware of the environmental problems. We can, and probably we must continue taking the lead. Let us then try to find innovative ways of putting science and practice together for the benefit of birds and mankind.

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PLENARY LECTURE

**RESPIRATION OF AVIAN EMBRYOS
AT HIGH ALTITUDES**

CYNTHIA CAREY

RESPIRATION OF AVIAN EMBRYOS AT HIGH ALTITUDE

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Boulder, CO 80309 USA

ABSTRACT. The ability of birds to colonize a wide diversity of habitats, including some of the most hostile ones of earth, depends in part upon the achievement of levels of gas exchange between the embryo and the environment within tolerance limits. The reduction in barometric pressure at high altitude causes avian embryos to develop in gaseous conditions that differ considerably from those at which embryos develop at sea level. Conservation of water appears to be a more important priority at moderate altitudes, whereas improvement of oxygen delivery becomes a primary selective force at higher altitudes. Modifications of eggshell conductance to gases compensate in part for variation in gaseous diffusion, particularly at low altitude, but specializations in embryonic physiological properties, such as blood oxygen carrying capacities and capillary density of the chorioallantoic membrane, play increasingly important roles in fostering growth and development at high altitudes.

Keywords: Avian egg, eggshell conductance, gaseous diffusion, pore area, avian reproduction.

INTRODUCTION

Birds are among the most successful vertebrates in terms of their ability to invade and to colonize a wide variety of habitats, including some of the most hostile ones. Their ability to do so has depended on their capacity to reproduce successfully in a variety of climatic conditions. Successful reproduction, particularly in hostile environments, requires a suite of specializations that foster survival of offspring through incubation, hatching, fledging, independence from the adults, and ultimately breeding themselves. Focusing specifically on embryos, survival to hatching depends importantly on whether the requirements of the embryo are met within its tolerance limits. Adults periodically turn eggs, provide heat, and defend eggs from predators (Drent 1975). The egg, prepackaged before laying, contains all the nutrients, water and ions the embryo needs for growth and development to hatching. The final embryonic requirement during incubation is for gas exchange between the interior of the egg and the external environment.

Twenty years ago, relatively little was known about embryonic gas exchange and its relation to avian biology. The pioneering work of Hermann Rahn, Charles Paganelli, Amos Ar, and their colleagues, who have combined to publish over 80 papers on the subject, has led to a veritable explosion of knowledge about avian eggs. The goal of this paper is to summarize a small part of this field by considering the interrelations of gas exchange, shell structure and embryonic physiological properties of species breeding at high altitudes.

GAS EXCHANGE AT SEA LEVEL

Before dealing with the particular problems encountered by avian embryos at high altitude, it is appropriate to review briefly the process of gas exchange in lowland embryos. The embryo exchanges O_2 , CO_2 , and water vapor with its environment (Wangensteen & Rahn 1970/71). These gases travel principally by the process of diffusion down partial pressure gradients (Wangensteen et al. 1970/71, Wangenstein 1972). The gradients for O_2 and CO_2 are established by the metabolism of the embryo; as it consumes O_2 and produces CO_2 inside the shell, partial pressures of these gases (pO_2 and pCO_2) inside the egg decrease and increase, respectively, relative to pressures outside the egg (Wangensteen 1972). A partial pressure gradient for water vapor (ΔP_{H_2O}) exists across the eggshell because the interior of the egg is fully saturated with water vapor, whereas the nest environment of almost all species, except those laying eggs in soil or rotting vegetation (Seymour & Ackerman 1980), is not fully saturated (Wangensteen & Rahn 1970/71). Oxygen travels into the egg while CO_2 and water vapor move outward through common pores in the shell (Paganelli et al. 1978).

The factors which determine the rate of diffusion of a gas (M , $cm^3STPD.sec^{-1}$) are described by a modification of the Fick equation (Wangensteen 1972; Paganelli et al. 1975):

$$M = (D/RT) \cdot (A_p/L) \cdot \Delta P \quad (1)$$

where D = binary diffusion coefficient ($cm^2.sec^{-1}$), RT = gas constant and absolute temperature ($cm^3STPD.cm^{-3}.torr^{-1}$), A_p = effective pore area (cm^2), L = length of diffusion path, or shell thickness (cm), and ΔP = partial pressure difference of gas across the shell ($torr$). The terms $(D/RT) \cdot (A_p/L)$ are often combined into the term "G" ($cm^3.sec^{-1}.torr^{-1}$) representing the conductance, or the diffusive capacity of the eggshell to each gas (Ar et al. 1974). Therefore, eq. 1 can be rewritten as:

$$M = G \cdot \Delta P \quad (2)$$

Conductance is conventionally reported as standardized to 760 torr so that G of a species can be compared with that of other species under identical conditions of pressure.

The fact that O_2 diffuses in the opposite direction from CO_2 and water vapor places opposing, or mutually antagonistic, requirements on the structure of the shell. The conductance must be large enough to allow sufficient O_2 to diffuse inward for support of metabolic requirements, but restrictive enough to prevent excessive losses of water vapor and CO_2 from the egg. Most workers have agreed that control of losses of water vapor and/or CO_2 has probably been a more important priority for eggshell design at low altitudes than has been maximization of O_2 delivery (Vleck et al. 1979, Vleck et al. 1980, Ar & Rahn 1980, Paganelli & Rahn 1984).

The role the shell plays in regulation of embryonic gas exchange is sufficiently important that G has apparently evolved in conjunction with two other interrelated traits: duration of incubation period (I) and egg mass (W). Ar & Rahn (1978) observed that

G is inversely proportional to I for a given W. If the eggs of two species have equivalent mass but different incubation periods, G will vary inversely with I with the result that total gas exchange of the two eggs will be comparable by the end of incubation (Ackerman et al. 1980). Conductance has also apparently evolved in conjunction with the gaseous environment in which the eggs of a particular species are laid. Average G of eggs laid in very humid, hypoxic, or hypercapnic environments is substantially larger than predicted on the basis of I and W (Lomholt 1976, Birchard & Kilgore 1980, Seymour & Ackerman 1980).

Therefore, the average G of a given species was presumably selected by differential mortality of embryos in eggs laid with excessively high or low conductance. However, relatively little is known about the tolerance limits of avian embryos.

Water loss during incubation achieves two important results: formation of an air cell at the blunt end of the egg and maintenance of relative hydration of contents. As water diffuses out of the egg, it is replaced by an equivalent volume of air (Romijn & Roos 1938). Just prior to pipping the shell, the embryo pips into the air cell and uses the volume to expand its lungs, thus beginning the conversion from diffusive to convective respiration (Vince & Tolhurst 1974). The egg contents of altricial and precocial eggs at laying are approximately 75 and 85% water, respectively (Ar & Rahn 1980). These relative hydration levels are maintained through pipping by water loss. The amount of water lost compensates for both the reduction in solids catabolized and the production of metabolic water (Ar & Rahn 1980).

Ar & Rahn (1980) have suggested that water loss from the egg must be precisely regulated within narrow limits for optimal hatching. This proposal is based on observations that the hatchability of Domestic Chicken (*Gallus domesticus*) embryos decreased markedly if too much or too little water is lost during incubation (Lundy 1969; Tullett & Board 1982) and that eggs lose about the same average amount of mass as water vapor (17%) during incubation (Ar & Rahn 1980). Apparently, only one study currently exists testing tolerances of embryos of wild species to variation in water loss: Red-winged Blackbird (*Agelaius phoeniceus*) embryos hatch successfully from eggs losing between 7.4 and 33.0% of initial mass and tolerate wider variations in G and daily water loss than are observed in populations of this species in the field (Carey 1976).

The interrelation of G, W, and I also results in general similarities in O_2 and CO_2 exchange for most species. The amount of O_2 consumed per g embryo (Ar & Rahn 1978) and the P_{O_2} and P_{CO_2} across the eggshell at comparable stages of incubation are similar in almost all lowland eggs (Rahn et al. 1974, Ar & Rahn 1978). Additionally, the final levels of O_2 and CO_2 in the air cell at pipping (PA_{O_2} and PA_{CO_2}) fall within narrow limits around 104 and 40 torr, respectively (Rahn et al. 1974, Hoyt & Rahn 1980). The importance of the latter two observations relates to the fact that the PA_{O_2} and P_{CO_2} prior to the onset of pulmonary respiration closely resemble those found in the lungs of hatchlings and adults (Tazawa et al. 1971, Wangensteen 1972, Rahn et al. 1974). Therefore, G not only regulates appropriate levels of gas exchange but also fosters preparation of the embryo for the onset of aerial respiration (Wangensteen et al. 1970/71, Rahn et al. 1974).

No experiments have yet tested the tolerances of embryos of wild species to variation in ambient P_{O_2} and P_{CO_2} , but hatchability of domestic fowl embryos severely declines if a small portion of the eggshell is blocked just prior to the onset of pulmonary respiration (Tazawa et al. 1971). Hatchability of domestic fowl eggs is severely reduced below 15% O_2 or above 40% CO_2 (Lundy 1969). Variation in ambient P_{O_2} could be especially detrimental for avian embryos, because it forms the upper end of the gradient for diffusion of O_2 through the shell and ultimately into the tissues.

GAS EXCHANGE OF EMBRYOS AT ALTITUDE

Biogeographers have suggested that existing montane populations of birds have descended from groups that have moved up and down altitudinal gradients as mountain ranges have risen or eroded and as global climatic changes have occurred (Mayr & Diamond 1976, Vuilleumier 1986). At least 27 species of birds are known to nest at altitudes between 4000 and 6550 m (Rahn 1977, Harris 1981, Carey et al. 1987, 1989a, b, 1990). Birds breeding at both high altitude and high latitudes face problems of cold, seasonality in food availability and snow cover (Carey 1988). The unique features of the montane environment are low barometric pressure and its associated consequences: hypoxia, low water vapor pressure, and intense ultraviolet light (Mani 1962).

Aggazzotti (1913) measured weight loss of some chicken eggs at Turin, Italy, and then again after transport to 2900 m on Monte Rosa. He found that the eggs lost substantially more weight at 2900 m than at low altitude and surmised that the excessive weight loss was due to increased water loss from the eggs. Rahn & Ar (1974) were the first to identify the cause of this phenomenon. As barometric pressure (P_B) decreases with increasing altitude, the diffusion coefficient (D in Eq. 1) increases inversely (Reid & Sherwood 1966, Paganelli et al. 1975, Paganelli 1980). Therefore, if Eq. 2 is rewritten with P_B representing the barometric pressure at the breeding location:

$$M = \frac{G(760)}{P_B} \cdot \Delta P \quad (3)$$

one can see that the "effective" conductance of an egg (G) for any gas will be higher at altitude than at sea level. If an egg is transported from sea level to roughly 5500 m, where the P_B is half that at sea level, losses of CO_2 and water vapor will be twice the amount at sea level, and O_2 will diffuse into the egg twice as rapidly (Paganelli et al. 1975). However, an increase in the diffusion rate of O_2 into the egg will only partially compensate for the fewer total number of O_2 molecules present in ambient air at low P_B (Visschedijk et al. 1980).

Since the data available on tolerance limits of low altitude embryos suggest that variation in gas exchange caused by the increase in D at altitude might prove detrimental, or even lethal, to embryos at high altitude, it is interesting to explore what mechanisms might compensate for the effect of D on gaseous diffusion (Rahn & Ar 1974).

If prevention of excessive water and/or CO_2 losses were the most important priority, one or more of the following might be implemented:

1. a decrease in G by increasing L or decreasing A_p , which would have the effect of increasing the resistance of the shell to gas diffusion;
2. a decrease in the $\Delta P_{\text{H}_2\text{O}}$ and ΔP_{CO_2} by raising $P_{\text{H}_2\text{O}}$ and P_{CO_2} in the nest environment. This could most easily be accomplished by increasing adult attentiveness on the nest and trapping these gasses in the nest microenvironment. (Note: use of either or both 1 and 2 will restrict availability of O_2 to the embryo);
3. increasing the initial water content of eggs and varying the buffering capacity of blood.

If optimization of O_2 delivery were the most important priority one or more of the following might be utilized:

- 1) an increase in G by decreasing L or increasing A_p , which would increase the resistance of the shell to diffusion of O_2 ,
- 2) an increase in ΔP_{O_2} by decreased nest attentiveness, (Note: use of either or both 1 and 2 would increase water and CO_2 loss),
- 3) an increase in O_2 delivery to the cells by an increase in blood O_2 carrying capacity, variation in hemoglobin oxygen affinity, increased capillarity of the chorioallantoic membrane, or other possible specializations at the cellular or biochemical level.

Moderate altitudes

The existing data comparing eggs laid by montane species with their conspecific or congeneric relatives nesting at sea level support the contention the conservation of water and/or CO_2 is the most important priority for birds colonizing montane habitats up to about 3600 m. A number of studies have indicated that the average conductance to water vapor ($G_{\text{H}_2\text{O}}$, standardized to 760 torr), of both domesticated chickens and montane populations of Red-winged Blackbirds *Agelaius phoenicius* and Robins *Turdus migratorius* breeding up to 3450 m progressively declined with P_b (Figure 1) (Rahn et al. 1977, Carey et al. 1983, Leon-Velarde et al. 1984a). A few other studies have shown either a decrease in $G_{\text{H}_2\text{O}}$ in montane eggs that did not parallel the reduction in P_b or even an increase with altitude (Packard et al. 1977, Sotherland et al. 1980, Taigen et al. 1980), but these studies used eggs of unknown age. Since $G_{\text{H}_2\text{O}}$ changes in early incubation in a number of species (see Carey 1983), the results could have reflected more the effect of egg age than an adjustment to altitude (see Carey 1980).

The decrease in $G_{\text{H}_2\text{O}}$ with increasing altitude to about 3600 m was largely attributable to a decrease in A_p than an increase in L (Rahn et al. 1977, Carey et al. 1983, Leon-Velarde et al. 1984). Shell thickness itself is under mutually antagonistic selective pressures; it must be strong enough to support the mass of the incubating adult, yet thin enough for the embryo to pip through the shell and hatch. It is likely that these constraints made it difficult to alter shell thickness as a mechanism for counteracting the change in gaseous diffusion coefficients at altitude.

By approximating the reduction in P_B , G_{H_2O} (standardized to 760 torr) compensates for the increase in D , with the result that the “effective” G_{H_2O} of montane eggs on the breeding grounds is the same as in lowland eggs. As a result, daily water losses from naturally incubated eggs of Red-winged Blackbirds and White-crowned Sparrows *Zonotrichia leucophrys* are independent of altitude to 3050 and 3660 m, respectively (Carey et al. 1983, Carey, unpubl. data). Therefore, these embryos develop in the same hydric environment as lowland embryos; without the decrease in G_{H_2O} (standardized to 760 torr), water losses would be at least 30% higher than they are. Relative water content of freshly laid eggs of Red-winged Blackbird and Robin eggs and adult attentiveness of Red-winged Blackbirds did not vary significantly from low altitude to about 2900 m (Carey et al. 1983).

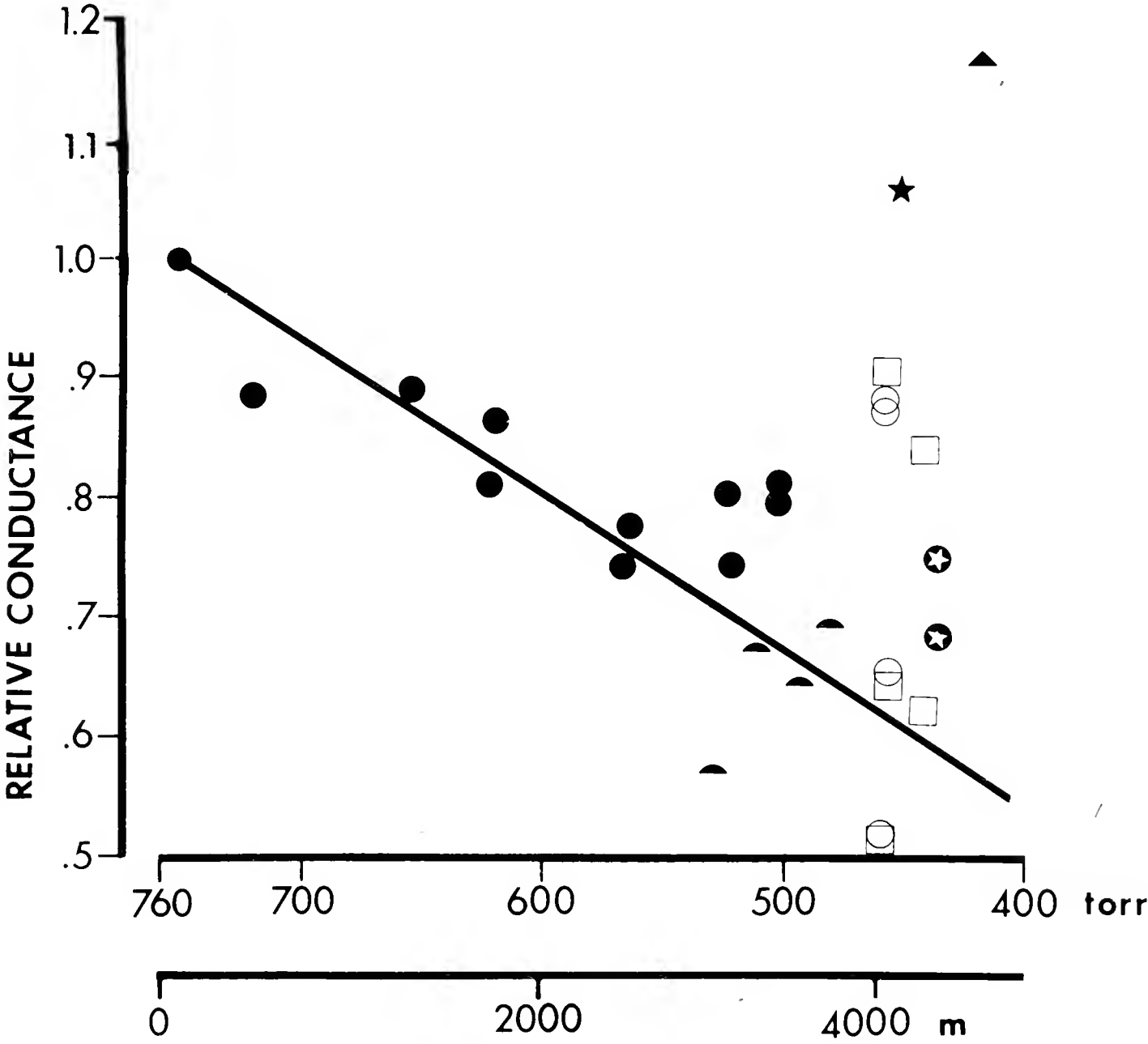


FIGURE 1 – Water vapor conductance (standardized to 760 torr) of eggs laid at various altitudes expressed as a proportion of the mean conductances of a sea level conspecific or congeneric species. The mean conductances of the sea level groups are set at 1.0. The line represents the predicted relative conductance at any altitude, assuming that the conductance equals 1.0 at sea level and is reduced in exact proportion to the barometric pressure. The symbols represent the following publications in which actual data on these species can be obtained: filled circles = *Agelaius phoeniceus* and *Turdus migratorius* (Carey et al. 1983); open circle in a filled square = *Larus serranus* and *Plegadis ridgwayi* (Carey et al. 1987); filled star = *Fulica americana peruviana* (Carey et al. 1989a); open circle = *Anas versicolor puna* (Carey et al. 1989b); open square = *Chloephapa melanoptera*, *Anas flavirostris oxyptera*, and *Rollandia rolland* (Carey et al., 1990); filled half circle = *Zonotrichia leucophrys* (Carey; unpubl. data); filled triangle = *Larus serranus* (Leon-Velarde et al. unpubl data).

Since the "effective" G at altitude approximated the comparable value at sea level, yet the total number of O_2 molecules in the ambient air at altitude are fewer, the air cell O_2 tension (P_{AO_2}) of Red-winged Blackbird eggs dropped progressively from about 80 torr at low altitude to about 50 torr at 2900 m (Carey et al. 1982). The P_{AO_2} serves as the upper end of the gradient for diffusion of O_2 into the blood (Wangensteen 1982). Low P_{AO_2} was associated with decreased oxygen consumption (Y_{O_2}), prolonged incubation periods, and decreased hatchling masses of chicken embryos at 3800 m (Wangensteen et al. 1974), but Y_{O_2} of Red-winged Blackbird embryos at 2900 m was statistically indistinguishable from that at lower altitudes, and hatchling masses and incubation periods of Red-winged Blackbirds, White-crowned Sparrows, and Horned Larks *Eremophila alpestris* were independent of altitude to 2900, 3475, and 3600 m, respectively (Carey et al. 1982). Therefore, it appears that control of water loss is the most important priority for shell design at altitudes up to around 3600 m. Presumably, loss of CO_2 from the shell would also be maintained at sea level values, although no studies have investigated CO_2 losses directly in eggs at moderate altitudes. Although availability of O_2 is limited by reduction of A_p , embryos apparently still get enough O_2 for normal metabolism and growth.

The question has been addressed whether the change in G_{H_2O} with altitude results from detection by the female of variation in P_B or one of its correlates, or whether the characteristic G of a population results from long-term selection for females laying a genetically-fixed shell appropriate for the physical conditions at the breeding location. Rahn et al. (1982) transported chickens from a breeding colony at 3800 m to 1200 m and found a significant increase in G_{H_2O} that approximated the increase in P_B . However, some statistical weaknesses existed in the data: unequal numbers of eggs from each female were pooled for comparison of low and high altitude groups, and data from females which didn't produce eggs at the lower altitude were included in the montane average. Other studies have found no effect of variation in P_B on G_{H_2O} . Leon-Velarde et al. (1984b) found no significant difference between average G_{H_2O} of eggs laid by chickens which had been transported from sea level to 2800 m within 24 hr after hatching and those laid by the sea level stock from which they had originated. Average G_{H_2O} of eggs laid by Bengalese Finches *Lonchura striata* and quail *Coturnix coturnix* did not change between sea level and after transport to 2900 m, when eggs of the same female were compared before and after transport (Carey et al. 1984). Therefore, it is probable that the reduction in G_{H_2O} observed in montane groups of chickens and wild birds most likely results from long-term selection for genetically fixed shell characteristics. Genetic control of shell features has also been documented by Sotherland et al. (1979) and Bucher & Barnhart (1984).

High altitude

We now move to consideration of the question concerning how birds breeding above 3600 m cope with the effect of increasing D on gaseous diffusion. The data suggest that priorities shift from conservation of water and/or CO_2 to improvement of O_2 delivery. Conductance (standardized to 760 torr) of eggs laid at higher altitudes is not decreased to the same extent as in barometric pressure at the breeding location (Figure 1). In fact, G of some montane species exceeds that of their lowland counterparts, resulting in a curvilinear relation between G and P_B . If G (standardized to 760 torr) of eggs laid at altitudes above 4000 m were reduced to the same proportion as P_B so

that the effective G at altitude was the same as at sea level, the amount of O_2 reaching the embryo would be inadequate to support costs of both maintenance and growth (Carey et al. 1989a). Most of the comparisons in Figure 1 for eggs laid above 4000 m were made with averages of montane eggs and those of similarly-sized eggs of lowland congeneric species (Carey et al. 1987, 1989b, 1990). These types of comparisons were necessitated by the fact that most species breeding at very high altitudes do not breed over broad altitudinal gradients and lack conspecific lowland populations. Therefore, probably the most accurate indication concerning how G_{H_2O} of a high altitude population compares with a lowland conspecific population is provided by American Coots *Fulica americana peruviana*. Average G_{H_2O} (standardized to 760 torr) of American Coot eggs laid at 4150 m was 107% of the sea level value, whereas P_B at the montane location was 60% of that at sea level (Carey et al. 1989a).

Since G of eggs of many species laid above 3600 m does not track the reduction in P_B at the laying location and undercompensates for the increase in D , the "effective" G , caused by the influence of D at altitude, is higher than that at sea level. As a result, water losses from naturally incubated eggs of American Coots at 4150 m and Andean Gulls *Larus serranus* and Puna Ibises *Plegadis ridgwayi* at 4400 m were substantially greater than that of their sea level counterparts. The effect of the higher rate of water loss on the embryo is difficult to assess because data on incubation periods of these montane groups, needed to calculate the total water loss during incubation, are not available. If incubation periods of these montane groups are equivalent to those of their lowland counterparts, Andean Gull and American Coot eggs at 4400 and 4150 m, respectively, would lose about 20 and 18%, respectively, of their initial mass as water vapor during incubation (Carey et al. 1987, 1989a). These percentages are well within the range for total water loss established for species breeding at low altitudes (Ar & Rahn 1980). Incubation periods of gulls and coots would have to be substantially prolonged for tolerance limits exhibited by Red-winged Blackbird embryos to be approached (Carey 1986). Relative water content of freshly laid and partially incubated Andean Gull and American Coot eggs fell within the range of values known for lowland precocial and semi-precocial eggs (Carey et al. 1987, 1989a). The lack of variation in relative water content of these montane eggs could result from one of at least two possible causes: 1) no selection has existed for adding extra water to the egg as a mechanism for offsetting increased water loss because embryonic tolerance limits are not taxed by the rates of water losses at these altitudes, or 2) dilution of egg content may cause mortality by interfering with cellular processes. Studies on eggs experiencing severe rates of water loss are necessary to discriminate between these or other possibilities.

Despite the improvement in effective G by an increase in A_p in eggs of some species laid above 4000 m (Carey et al. 1987, 1989a, 1989b), montane embryos develop in a hypoxic environment. In fact, variation in shell characteristics plays an increasingly less important role at higher altitudes because no possible adjustment can create gaseous conditions similar to those at sea level. Instead, embryonic physiological properties become increasingly more important for adjusting to abnormal gaseous conditions inside the shell. The P_{IO_2} , or the "effective" O_2 tension outside the egg at sea level is approximately 148 torr (Wangensteen & Rahn 1970/71). The P_{AO_2} inside an egg declines from approximately that value in freshly laid eggs to about 100 torr,

or slightly less in small eggs, by the end of incubation due to the increased demand for O_2 by the growing embryo (Wangensteen 1972, Vleck et al. 1979, Hoyt & Rahn 1980, Bucher & Barnhart 1984). The P_{IO_2} at 4150 m is roughly 84 torr (Carey et al. 1989a). The P_{AO_2} of the aircell of fresh montane eggs approximates 84 torr and then declines from that level during incubation (Carey et al. 1989a, 1991a). Therefore, even at the beginning of incubation, the P_{AO_2} of montane eggs is substantially below that of lowland eggs at the end of incubation.

Embryonic oxygen consumption (Y_{O_2}) in such hypoxic environments has exhibited two types of patterns. One pattern is illustrated by chicken and American Coot embryos at 3800 and 4150 m, respectively; Y_{O_2} was depressed compared to that of their lowland counterparts (Wangensteen et al. 1974, Carey et al. 1989a). The growth rates of chicken embryos were slower and hatchling masses were smaller than those of their sea level relations (Wangensteen et al. 1974). Embryonic masses of American Coots at 4150 m were similar to, but their incubation periods were probably longer than those of lowland American Coots (Carey et al. 1989a). Wangenstein et al. (1974) have hypothesized that the depressed Y_{O_2} of montane chicken embryos is an adaptation which maintains the P_{AO_2} as high as possible with the result that the ΔP_{O_2} driving O_2 into the blood as large as possible. However, since prolongation of the incubation period exposes eggs to greater risks of predation and since smaller hatchlings are often at a disadvantage for survival (Packard 1990), an alternative explanation for the low Y_{O_2} is that montane chick and coot embryos are unable to obtain sufficient O_2 for maintenance of normal growth and metabolism in the hypoxic environment inside the shell. Chicken embryos are remarkably sensitive to hypoxia. Hatchability decreases below sea level values at altitudes as low as 1600 m and drops to extremely low levels above 3000 m (Moreng 1983, Leon-Verlarde et al. 1984a). Coot embryos appear quite viable and hatchability seems high at 4150 m (Carey et al. unpublished data). Since American Coots breed over altitudinal gradients of at least 4150 m in the Peruvian Andes, the depressed Y_{O_2} of montane coot embryos may be symptomatic of the effect of gene flow from lower altitudes which may prevent genetic specializations to the physical environment at high altitudes.

The other pattern in Y_{O_2} is exhibited by Puna Teal *Anas versicolor puna* embryos. The level of Y_{O_2} of these individuals was comparable to that of lowland chickens, and in fact, was higher at comparable embryonic masses than the Y_{O_2} of lowland American Coots (Carey et al. 1989a, 1991a). While comparative data on hatchling masses of Puna Teal embryos are not available, the incubation period of montane eggs appears to be similar to that reported for a captive population held at sea level for several generations (Carey et al. 1991a). The distribution of Puna Teal is largely limited to the high Andes; they are replaced at lower altitudes by Silver Teal *Anas versicolor* (Blake 1977). Their limited altitudinal distribution appears to have fostered development of specializations that improve abilities to maintain "normal" levels of Y_{O_2} in very hypoxic environments.

Puna Teal embryos are able to maintain higher Y_{O_2} at all embryonic masses than American Coot embryos despite having a smaller pressure head (P_{O_2}) for diffusion of O_2 into the blood; P_{AO_2} of 15 g Puna Teal and American Coot embryos was approximately 43 and 55 torr, respectively (Carey et al. 1989a, 1991a). However, this differ-

ence in P_{O_2} does not result in a difference in the P_{O_2} of arterialized blood (P_{AO_2}) of embryos of these two species, because Puna Teal eggs have a smaller resistance to O_2 diffusion between the air cell and the chorioallantoic blood. Chicken embryos at sea level have a large P_{AO_2} - P_{aO_2} difference of approximately 52 torr which can be decreased to some extent in hypoxic conditions (Piiper et al. 1980). The cause of this large resistance is hypothesized to be either a small arteriovenous shunt or a water layer between the inner shell membrane and chorioallantoic membrane, in which O_2 is relatively insoluble (Piiper et al. 1980). The P_{AO_2} - P_{aO_2} difference of montane American Coot and Puna Teal 15g embryos was about 25 and 10 torr, respectively (Carey et al. 1991a, 1991b). The mechanism by which this resistance is lowered in these two species is unknown.

Vertebrates in hypoxic circumstances increase the oxygen-carrying capacity of blood with a variety of mechanisms. Compared with values from low altitude congeneric or conspecific groups, adult birds living all or part of the year at 3000 m exhibited significantly higher hematocrits, red-blood cell counts, and hemoglobin concentrations, although it is unclear whether these differences were a response to hypoxia, prolonged cold, or both (Carey & Morton 1976). Chicken embryos significantly increased hematocrit after the shell was partially covered with a material impermeable to O_2 (Tazawa et al. 1971). Hematocrits of montane Andean Coot embryos were slightly higher at all embryonic masses than were those of their lowland counterparts (Carey et al. 1991b). Hematocrits of 16g Puna Teal embryos were higher than those reported for 18-day chicken embryos and for Canada Goose *Branta canadensis* and Bar-headed Goose *Anser indicus* embryos incubated at 1600 m (Snyder et al. 1982, Carey et al. 1991a). Other possible mechanisms of enhancing oxygen delivery to the cells, such as hemoglobin O_2 affinity, genetic variation in hemoglobin, effect of organic phosphates on hemoglobin affinity, variation in blood flow, myoglobin concentrations, and capillary density of the chorioallantoic membrane, have not yet been investigated in embryos of wild birds at altitudes. Genetic differences in hemoglobin and hypoxia appear to be particularly likely features in which specializations of montane embryos could be identified (Baumann 1984).

Despite the specializations which may exist for maximizing O_2 -carrying capacity of the blood of montane American Coot and Puna Teal embryos, the P_{O_2} of the venous blood returning from the tissues to the chorioallantoic membrane ranges from about 3 to 10 torr in mid- to late incubation (Carey et al. 1991a, 1991b). Since venous oxygen tensions are thought to reflect the P_{O_2} of the tissues (Tenney 1974), these embryos have the remarkable ability not only to maintain life but also to grow at tissue oxygen tensions that would be lethal on a prolonged basis for adult birds and mammals. Specializations at the cellular and biochemical level which foster this ability have not yet been identified.

Carbon dioxide production increases with embryonic mass throughout all or most of incubation as an end product of aerobic metabolism (Wangensteen 1972). The increase in D resulting in the higher effective G at high altitudes causes CO_2 to diffuse more rapidly from the egg than at sea level. As a result, the air cell P_{CO_2} (P_{ACO_2}) of montane American Coot eggs was about 10-20 torr below that of their lowland counterparts by the end of incubation (Carey et al. 1989a). The P_{ACO_2} of Puna Teal eggs

was higher at any given embryo mass than that of the coot eggs due to the higher rate of CO_2 production (Carey et al. 1991a). The P_{ACO_2} forms the lower end of the gradient for diffusion of CO_2 from the blood into the air cell, and, as such, plays an important role in determining blood pH. Despite the differences between P_{ACO_2} of montane coot and teal and lowland coot and chicken values, blood pH of the montane embryos did not differ significantly from lowland values (Tazawa 1971, Carey et al. 1991a, 1991b). Achievement of constant blood pH at different P_{CO_2} is probably due to a reduction in the $[\text{HCO}_3^-]$ in the blood of montane embryos, but the mechanism by which this occurs is unknown.

CONCLUSIONS

The modifications in the eggshell of eggs laid at moderate altitudes result in rates of water loss and probably CO_2 loss that are similar to those at low altitudes, at the cost of reduction in the P_{O_2} inside the shell. Despite such hypoxia, embryos at moderate altitudes are able to maintain levels of Y_{O_2} that promote normal development and hatching. At altitudes above 3600 m, apparently oxygen levels become limiting enough that selection promoted a relatively larger pore area than at moderate altitudes for some species. This adjustment increased availability of oxygen to the embryo at the cost of increased rates of losses of CO_2 and water vapor. The curvilinear relationship between G and P_{B} is one of the few examples in biology in which a linear environmental stress is associated with a reversal of an adaptation. This reversal results from a shift in priorities from conservation of water vapor and CO_2 at lower altitudes to improvement of O_2 availability at higher ones. At altitudes over 4000 m, no adjustments in shell features can produce gaseous conditions that are similar to those at sea level; as a result, embryonic physiological properties play a progressively important role in promoting survival and growth in gaseous conditions that would be lethal for certain lowland species.

No information is available on eggs or embryos of species breeding over 4600 m. Hopefully, further research will provide information on the remarkable specializations fostering successful reproduction at these altitudes which are certain to exist in these groups.

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PLENARY LECTURE

**CONSTRAINTS ON REPRODUCTION
IN ALBATROSSES**

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CONSTRAINTS ON REPRODUCTION IN ALBATROSSES

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ABSTRACT. The interplay of ecological, behavioural and physiological (chiefly endocrine) factors in regulating the reproductive rate of albatrosses (chiefly Wandering, Black-browed and Grey-headed Albatrosses at South Georgia) is reviewed. The focus is on three key processes: acquisition of breeding status, breeding frequency and breeding success. Hormonal and related physiological mechanisms preventing sexual maturity persist longer in females than males; acquisition of social maturity takes several more years. Age of first breeding depends on rate of pair formation which chiefly reflects the ability of males to spend time displaying at nests ashore (i.e. foregoing foraging). In basically biennial-breeding species endocrine mechanisms preclude females from breeding in years following success in rearing a chick; males are not restricted in this way but are constrained by behavioural factors. Even first-time breeders only show small reductions in breeding success and efficiency compared to experienced birds. This is unusual amongst seabirds and suggests that most necessary experience has been acquired during the long periods of immaturity and pair formation. Costs of reproductive strategies and tactics in survival terms cannot be adequately assessed, partly because full life-time reproductive success data are unavailable and partly because of major demographic changes over recent decades directly affecting adult and juvenile survival, consequent on incidental mortality associated with fisheries.

Keywords: Wandering Albatross, Black-browed Albatross, Grey-headed Albatross, *Diomedea*, *D. exulans*, *D. melanophris*, *D. chrysostoma*, ecology, behaviour, physiology, endocrinology, sexual maturity, pair-formation, social maturity, breeding frequency, breeding success, survival, South Georgia, Iles Crozet.

INTRODUCTION

The principal decisions facing a bird contemplating reproduction are how to acquire a partner, at what age (or time) to start breeding, how often to breed, how many eggs to lay and how to maximise and/or optimise the success of each breeding attempt.

Many of these problems are inter-linked and all involve interplay of a complex suite of ecological, ethological and physiological factors. Most detailed experimental investigations of reproductive strategies and tactics have been conducted on small passerines (e.g. tits Paridae - McCleery & Perrins 1988, Nur 1988, Tinbergen & Daan 1990), which have the advantage of short generation times and relative ease of handling and measurement but the complication of large and variable clutch sizes. Despite their considerable longevity and long generation times (greatly delaying acquisition of data on lifetime reproductive success), large non-passerines offer advantages of small and often fixed clutch size and their large size may enhance visibility, recognition of individuals by observers and have advantages for certain types of experimental physiology in the field.

Albatrosses, with their long delay before starting breeding, typically biennial breeding in several species, single-egg clutch and extreme longevity are often regarded as a paradigm of K-selected species. However, for seabirds in general and albatrosses

in particular there has been little synthesis of information with respect to these adaptations. This paper is a preliminary review of the relationships between ecological, behavioural and physiological (chiefly endocrine) factors in regulating the reproductive rate and performance of albatrosses. It focuses on three processes: acquisition of breeding status, breeding frequency, and breeding success. It concludes by considering factors influencing survival - the most important characteristic of all in determining productivity in long-lived birds.

SITES AND SPECIES

This paper draws chiefly on research conducted at Bird Island, South Georgia, significantly supplemented by material from French studies at Iles Crozet. It features principally the Wandering Albatross *Diomedea exulans* and subsidiarily the Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. chrysostoma* (Table 1). The last two species belong to the main element of the genus *Diomedea*, often referred to as mollymawks. They are sexually monomorphic, breed in large, dense (often mixed) colonies on grassy slopes or cliffs at sub-Antarctic islands. Wandering Albatrosses are one of two-three species referred to collectively as great albatrosses. They are twice the size of mollymawks, sexually dimorphic in size and plumage, and breed in dispersed colonies usually on flat or gently sloping grassland at sub-Antarctic islands. All species have very long reproductive seasons but only in the great albatrosses do these attain or exceed one year.

TABLE 1 - Duration of breeding season events in Wandering, Black-browed, and Grey-headed Albatrosses at South Georgia.

Species	Weight		Prelaying attendance	Incubation	Chick rearing	Total attendance	Breeding frequency
	Male	Female					
Wandering Albatross	10.6	9.0	27	78	278	383	Biennial
Black-browed Albatross	3.9	3.7	16	68	116	200	Annual
Grey-headed Albatross	3.8	3.6	26	72	141	239	Biennial

ACQUISITION OF BREEDING STATUS

Albatrosses have one of the longer periods of sexual immaturity known in birds, with some individuals not joining the breeding population until older than 15 years of age (Croxall 1982, Weimerskirch & Jouventin 1987, Weimerskirch et al. 1987). Even the average individual returns to its natal colony some five years before its first breeding attempt. The role of physiological (endocrine) and behavioural factors in the process of maturation, pair-bond formation and breeding has been best studied in the Wandering Albatross but all the evidence indicates that it is broadly similar in the other species.

Endocrine processes

For male Wandering Albatrosses, Hector et al. (1986a) showed that the amplitude of the testicular cycle (in terms of both testis size and testosterone concentration in the blood) increases with age up to about age 10 years (Figure 1). However, for males of age four-five years, the size of the testis and levels of circulating testosterone at

the appropriate time are amply sufficient for them to be regarded as physiologically sexually mature. For females, however, birds younger than age seven years show high and variable progesterone levels and low concentrations of oestradiol and luteinising hormone (LH) and are physiologically incapable of breeding. In contrast, older breeding birds have consistently low levels of progesterone and high levels of oestradiol and LH (Hector et al. 1986a, 1990).

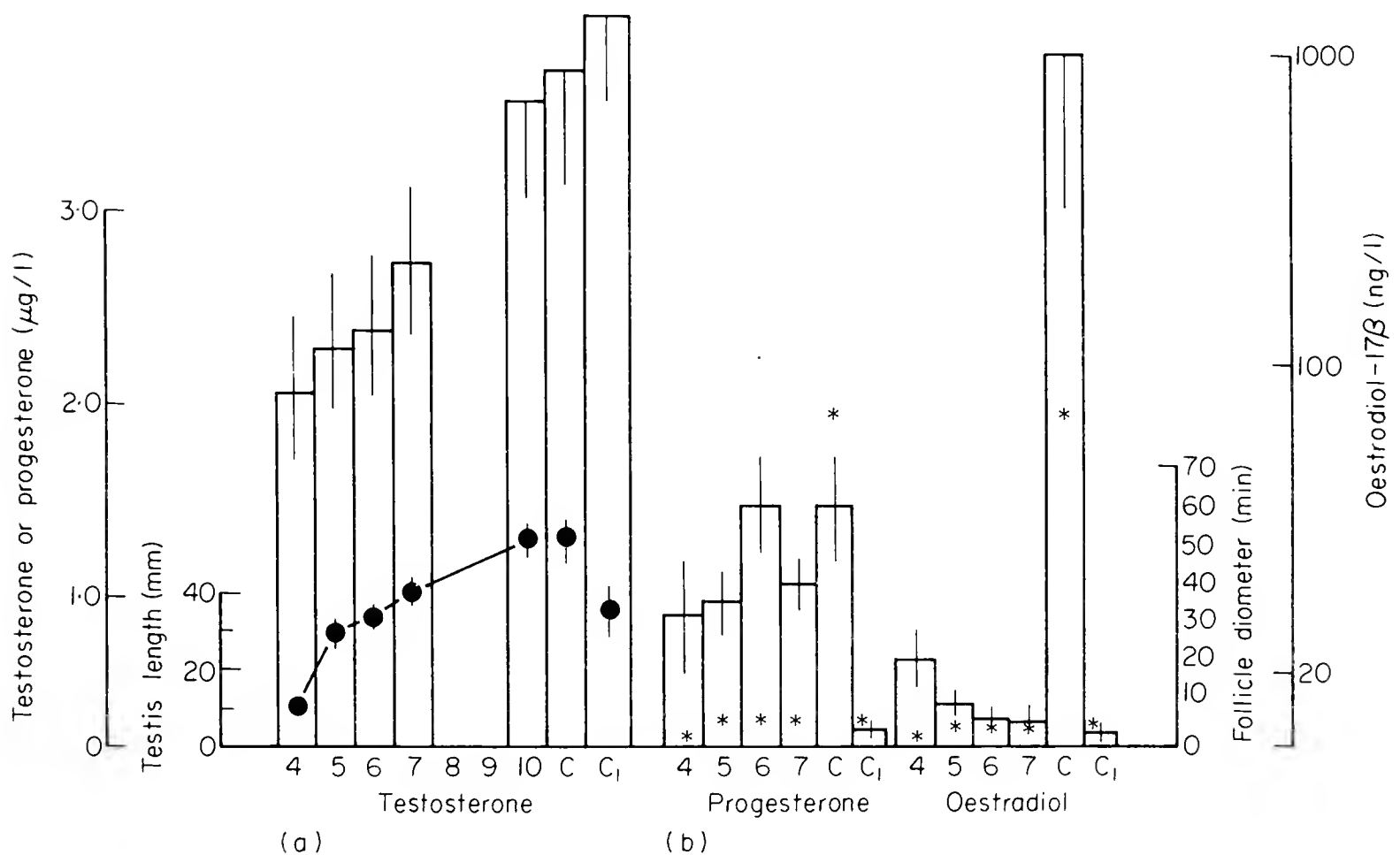


FIGURE 1 - (a) Maximum testicular length (•) (\pm standard error; $n > 3$) and concentrations of circulating testosterone in different age classes of immature male Wandering Albatrosses (\pm standard error of the mean; $n > 8$). The age classes, in years, are given on the bottom axis. Data from breeding birds caught at copulation (C) and at the same time as the non-breeding samples (C₁) are shown for comparison ($n = 6$ on both occasions). (b) Maximum diameter of largest follicle (*) and concentrations of circulating oestradiol and progesterone in different age classes of immature female Wandering Albatrosses (\pm standard error; $n > 9$). Categories C and C₁ are as for males ($n = 6$ on both occasions). (After Hector et al. 1986a).

These findings led to the suggestion (Hector et al. 1986a) that the ovary secretes progesterone rather than oestradiol to prevent vitellogenesis and egg formation, while regulating LH secretion by negative feedback. Subsequent experiments (Hector et al. 1990) showed that the progesterone was of ovarian origin and that, in response to LH injection, non-breeding birds secreted only progesterone but those birds about to lay eggs secreted both progesterone and oestradiol (Figure 2).

Whatever the precise interactions within the hypothalamus-pituitary-gonad axis and the exact role of progesterone in the inhibition of egg-laying, it seems clear that physiological sexual maturity in female Wandering Albatrosses is not attained before seven years of age. This is entirely consistent with field data, whereby in 1500 records only 2% of females have laid at age seven years and none at an earlier age. Remarkably, this situation has been maintained even though the average age of first breeding has

been decreasing in recent years (Croxall et al. 1990). Thus the physiological barrier has been maintained in the face of ecological/behavioural pressure towards an earlier age for first breeding.

Behavioural processes

Physiological sexual maturity does not necessarily guarantee immediate maturity in the social context, because even albatrosses of appropriate age take several years to acquire partners and breed (Pickering 1989).

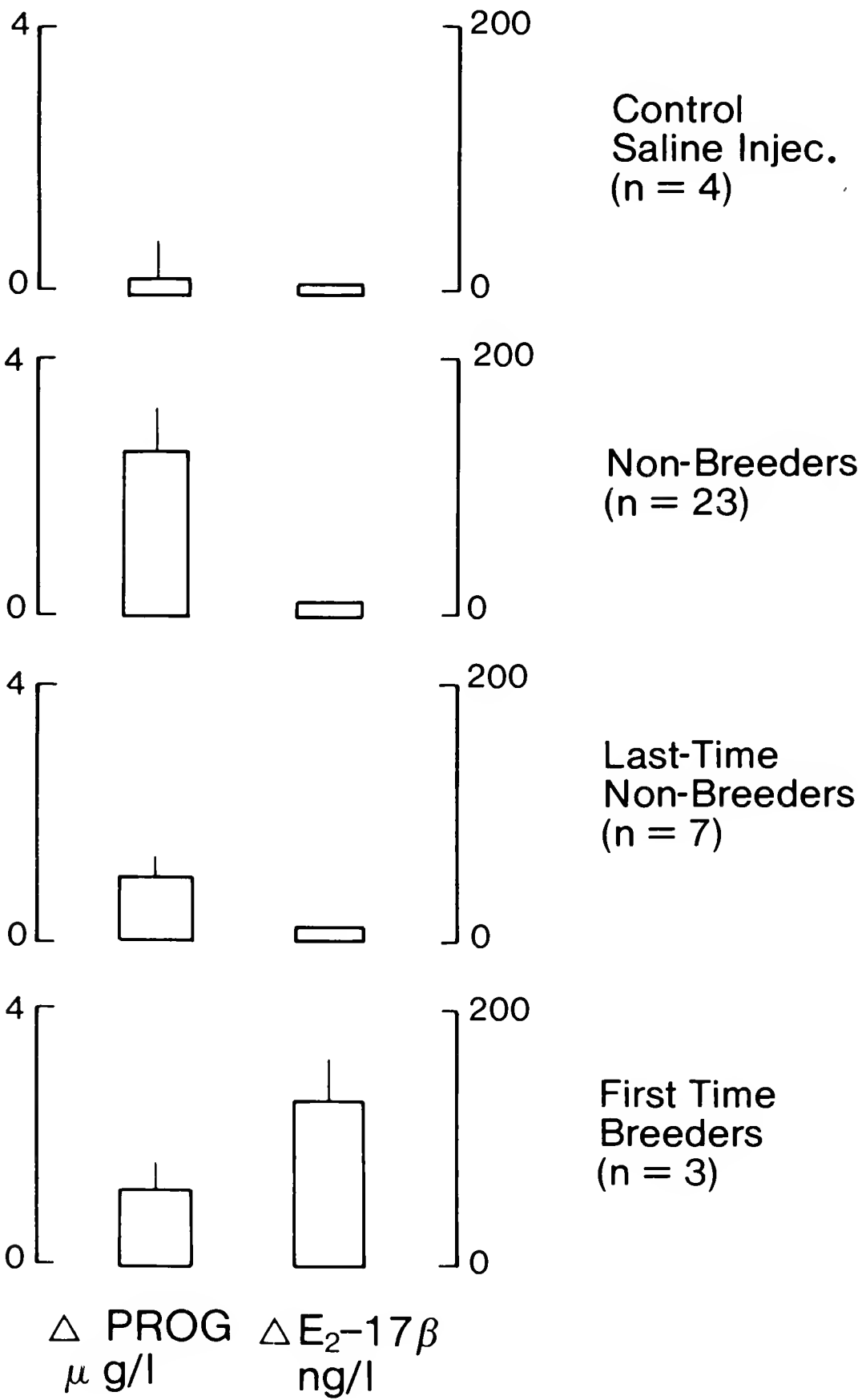
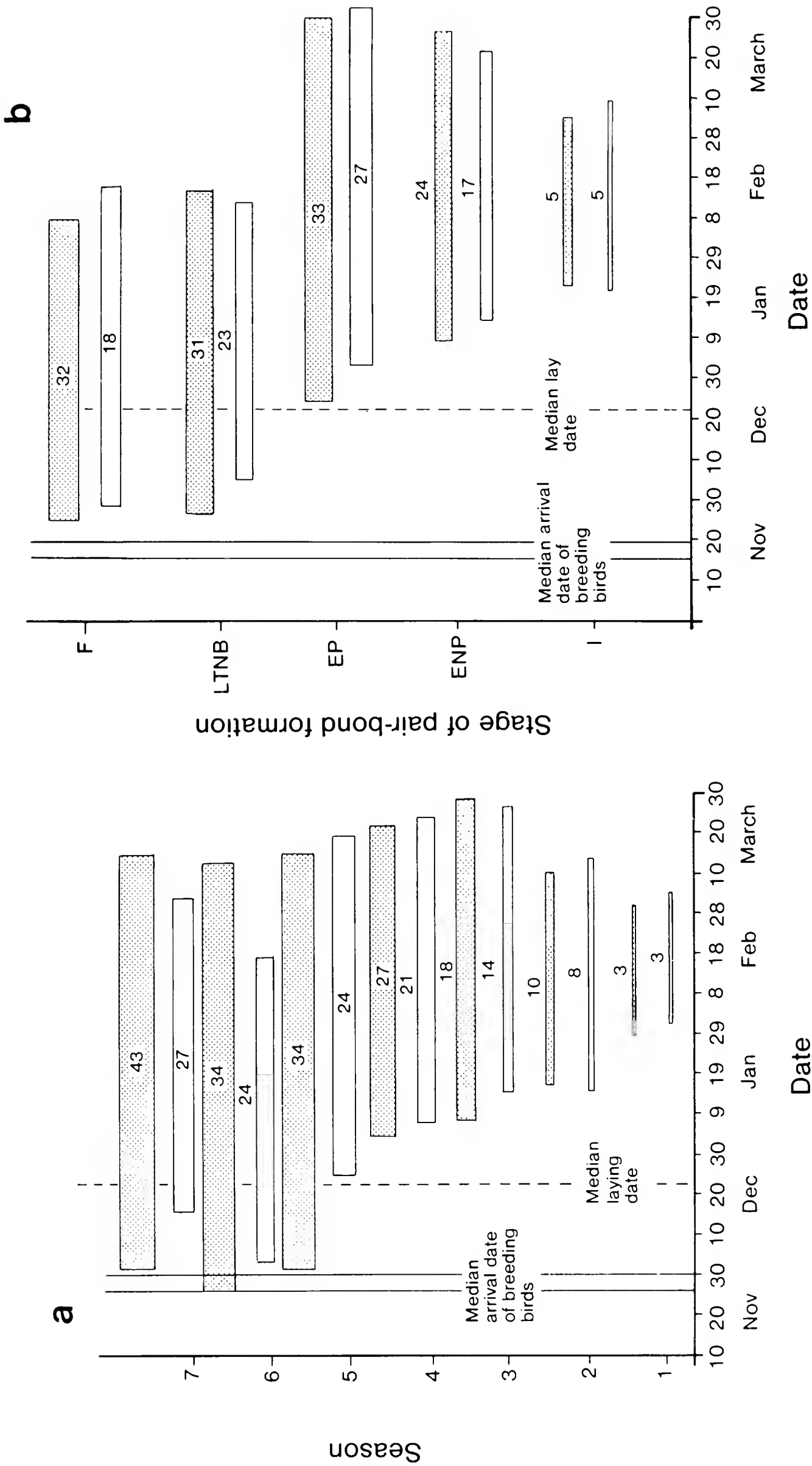


FIGURE 2 - Change in progesterone and oestradiol concentration after a single injection of ovine LH in four separate groups of female Wandering Albatrosses. Values are mean \pm standard error. (After Hector et al. 1990).

FIGURE 3 - Attendance patterns of Wandering Albatrosses: (a) in relation to experience. Each horizontal bar spans the median arrival to median departure date. Its thickness is proportional to the number of days ashore. The median number of days ashore is shown within or above each block. Males (stippled), females (clear) ($n = 393$). (b) in relation to stage of pair bond formation. I: Inexperienced birds; ENP: Experienced non-pairing birds; EP: Experienced pairing birds; LTNB: Last-time non-breeders; F: Former breeders. Other conventions as in Figure 3a ($n = 421$). (After Pickering 1989).



Wandering Albatrosses of both sexes first return to Bird Island (and, indeed, to their natal area on the island) at an average age of five years (range 3-12 years). On their first visit they arrive some two months after the median laying date and stay for only three days on average. In each succeeding year they arrive earlier and stay longer (Figure 3a). In relation to their stage of pair-bond formation (Figure 3b), however, the critical change comes between experienced pairing birds (i.e. birds seen together regularly at a nest site), none of which arrive before the median laying date, and last-time non-breeders, whose pattern of arrival and attendance is similar to that of former breeding birds (Pickering 1989). At all ages and in all categories females spend significantly less time ashore than males.

The actual process of pair formation proceeds through various stages. Initially, with increasing experience (time spent ashore), birds spend more time displaying and interact with more birds of the opposite sex (Figure 4). Subsequently displays are performed with increasing frequency with a decreasing number of partners (Figure 4) and increasingly often at the site of a nest built by the male bird (Pickering 1989).

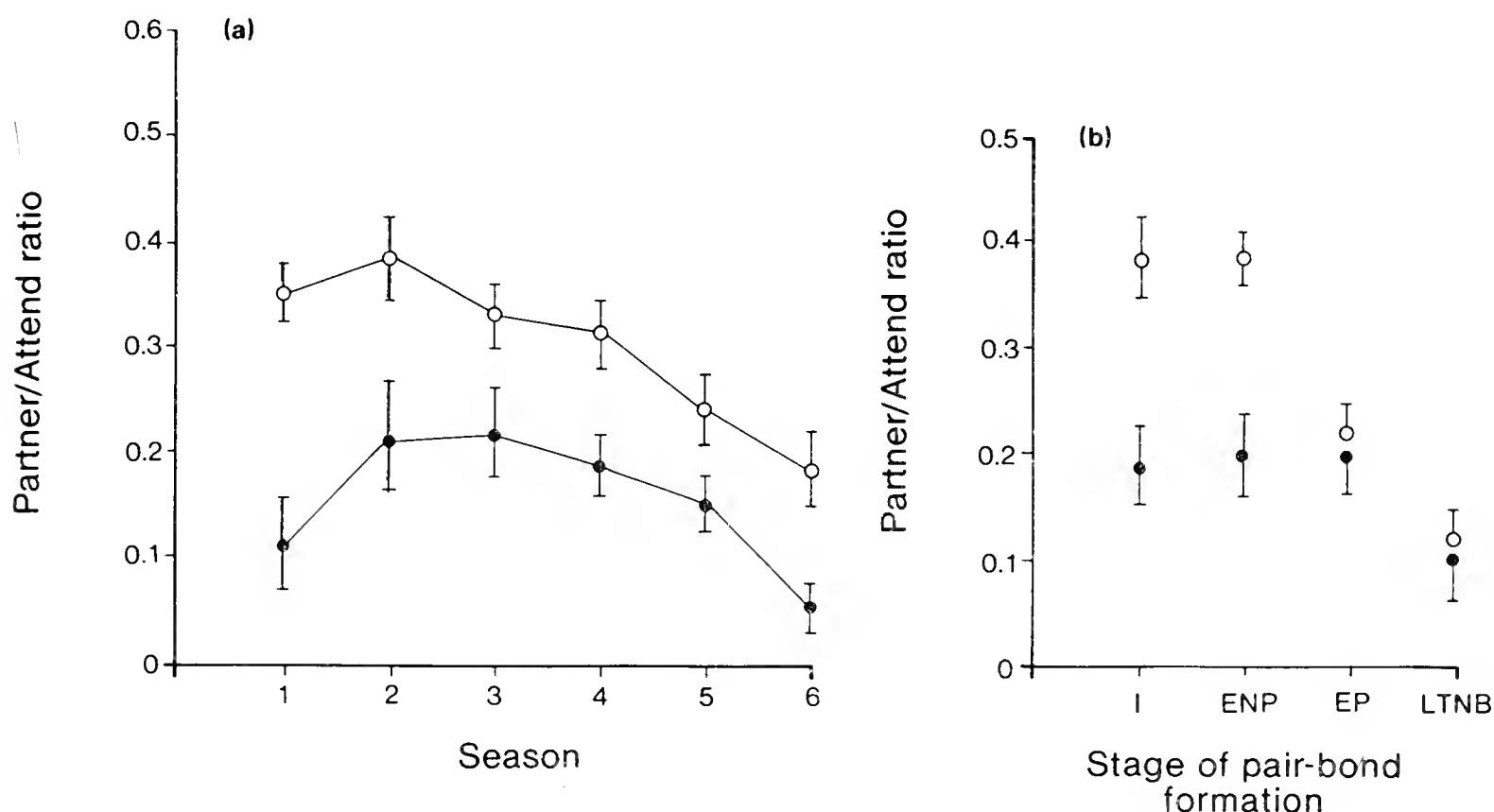


FIGURE 4 - Partner/attend ratio (number of different partners divided by total number of days ashore) in relation to (a) experience (number of seasons) and (b) stage of pair bond formation, among Wandering Albatrosses. Values are means, vertical line one standard error: males (•); females (o) (n = 338). (After Pickering 1989).

The process of refinement of sexual interaction ashore offers considerable potential for the assessment of mate quality, in particular by females whose role in mate choice is ultimately decisive. The spectacular vocal and visual displays of Wandering Albatrosses, the progressive whitening of their plumage with age and the fact that this happens more rapidly in males than females (Weimerskirch et al. 1989) would seem to offer substantial possibilities for potential as indicators of mate quality. However, an intensive investigation of the frequency and intensity of vocal and visual displays and of the size and plumage characteristics of males showed no significant relationship between any of these characteristics, singly or in any combination, and the ultimate choice of partner (S P C Pickering unpublished data). The only characteristic which was consistently related to the likelihood of pair formation was the time spent

ashore, and especially the time spent at the nest site, by the male. Thus the more time males spent at their nest, the more likely they were to be present when any particular potential female partner arrived; consequently they were even more likely to spend time displaying with this female and time spent displaying was the main precursor to, and best predictor of, subsequent pair formation.

Despite this unspectacular result, from the perspective of the female the frequency with which a male is encountered on her periodic, unpredictable and relatively brief visits ashore, may still be as good an index of quality as any other. In spending time ashore, males are not foraging at sea. Therefore males which spend longer periods ashore are also inferentially indicating their superior foraging (or fasting) abilities. The fact that over several consecutive years time spent ashore is brief and increases only slowly with age suggests that the cost of spending time away from the feeding ground is not trivial. The acquisition of the ability to sustain lengthy fasts ashore is clearly a crucial precursor to embarking on the lengthy pre-laying attendance and incubation shifts required by birds (especially males) attempting to breed (Croxall & Ricketts 1983).

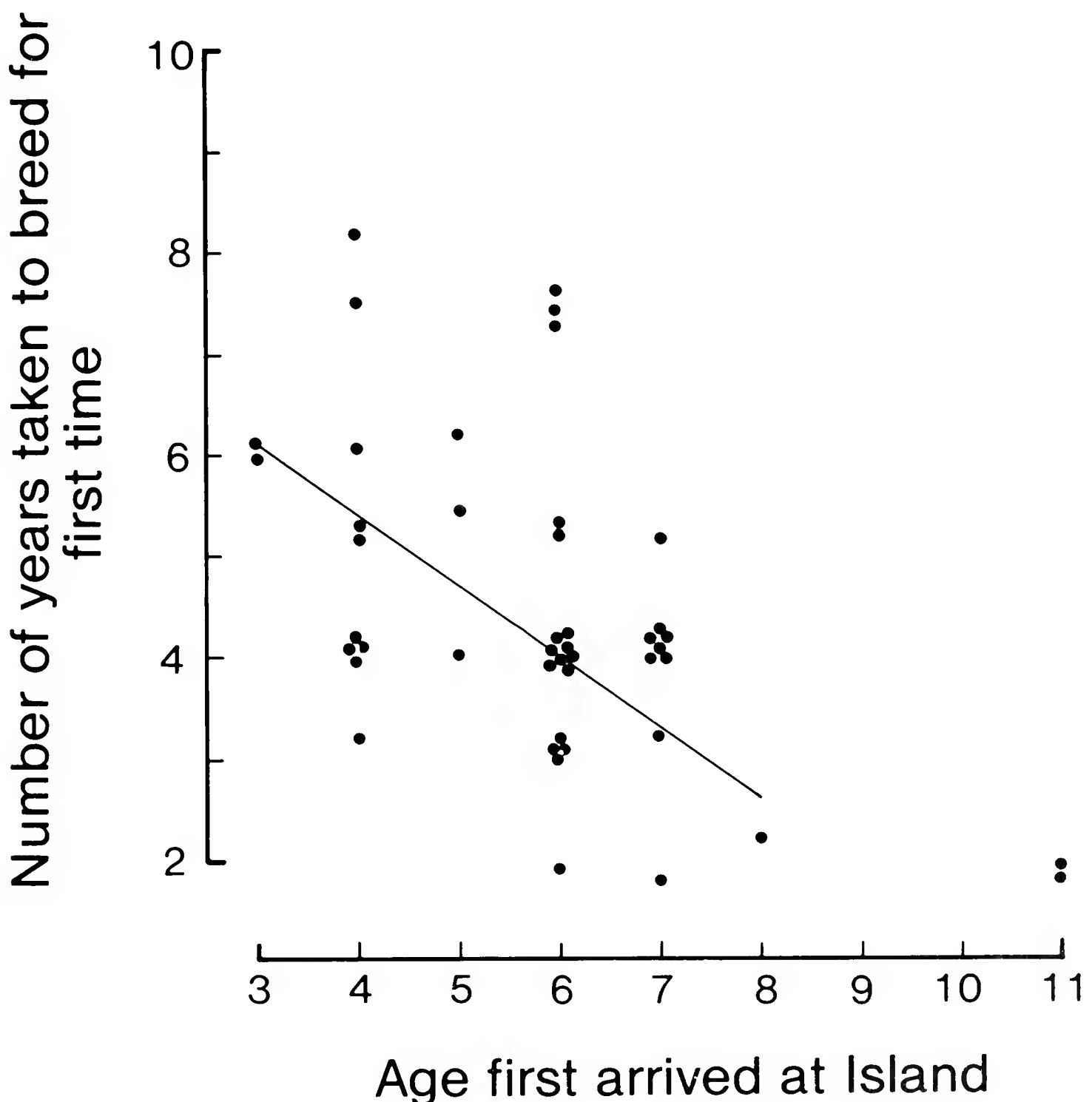


FIGURE 5 - Time (years) between arrival and first breeding in female Wandering Albatrosses in relation to their age on first return to Bird Island. The solid line indicates the slope of the regression equation. (After Hector et al. 1990)

In the process of reaching breeding status a number of constraints have to be overcome and the nature of these are different for each sex. Thus males attain physiological sexual maturity around the age at which they first return to their future breeding area; females take several more years to reach this state. Nevertheless, it seems that the behavioural interactions are decisive in determining when breeding first occurs. Males invest more time than females in being available for these interactions but it is the female that has the pre-eminent role in determining when a persistent association at a specific nest site develops. The key to preparation for successful reproduction, therefore, is the ability to spend lengthy periods ashore. Time ashore in the last year before breeding, however, is still only about 60% of that required by the end of the incubation period in a normal breeding season, so the timing of the transition (i.e. when to make the first breeding attempt) is clearly important. A naive expectation might be that birds which come ashore at the earlier ages will achieve breeding status before those which first attend at older ages. However, Hector et al. (1990) showed that the reverse was generally true (Figure 5). This is chiefly because birds arriving at older ages spend much more time ashore in their first two years of attendance than do younger birds (Figure 6).

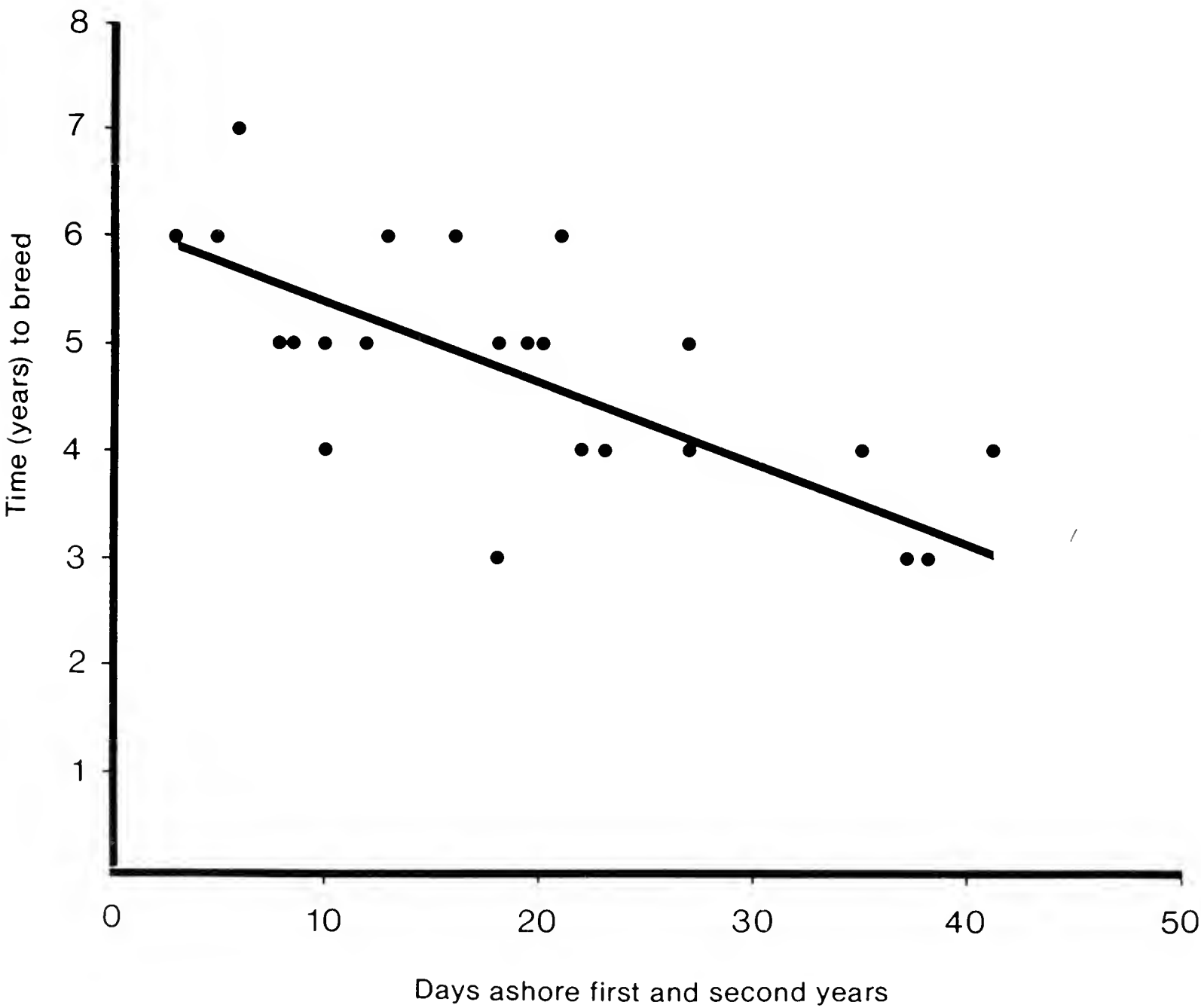


FIGURE 6 - Time (years) between arrival and first breeding in Wandering Albatrosses at South Georgia in relation to time (days) spent ashore in their first and second years after arrival.

To the inter-play between physiological and behavioural competence is thus added the ability to divert time away from energy-gathering activities; it may well be that this is the most decisive factor of all in determining when an albatross is likely to start breeding.

FREQUENCY OF BREEDING

Although it is usually surmised that most mollymawks breed annually, adequate published evidence is available only for Yellow-nosed Albatross *Diomedea chlororhynchos* (Jouventin & Weimerskirch 1988), Buller's Albatross *D. bulleri* (Richdale & Warham 1973) and Black-browed Albatross (Tickell & Pinder 1975, Prince 1985). All great albatrosses, both species of *Phoebetria* (sooty albatrosses) and the Grey-headed Albatross are known to breed biennially if successful in rearing a chick but approximately annually if unsuccessful (Tickell 1968, Tickell & Pinder 1975, Weimerskirch 1982, Prince 1985). Despite considerable variation between years (Figure 7, Table 2), the average values give a realistic representation of the differences between species (Table 2).

TABLE 2 - Breeding frequency of Wandering, Black-browed and Grey-headed Albatrosses at South Georgia. Values are means (based on ten or more years data - from Croxall et al. 1990; Prince 1985 and unpublished), with range in parentheses.

Species	Status*		Subsequent year			
			n + 1	n + 2	n + 3	n + ≥4
Wandering Albatross	Fail	(36)	63 (36-75)	17 (7-43)	8 (5-13)	
	Success	(64)	0	66 (55-75)	13 (4-20)	7 (5-9)
Black-browed Albatross	Fail	(63)	75 (58-87)	9 (4-25)	5 (0-16)	
	Success	(37)	81 (57-93)	7 (0-19)	4 (0-18)	
Grey-headed Albatross	Fail	(54)	54 (26-80)	24 (12-51)	9 (3-23)	
	Success	(46)	1 (0-2)	68 (31-88)	10 (5-32)	7 (0-19)

* Values in parentheses are average percentage in each category.

Thus for Black-browed Albatross there is no significant difference between the breeding frequency of birds that are successful or not in rearing chicks. A relatively small proportion of birds whose partners are still alive defer breeding by more than one year. The other two species exemplify the biennial strategy, with most successful and unsuccessful breeders making their next attempt two or one years later respectively but with a significant proportion in both cases deferring by longer than this. The only significant difference between Grey-headed and Wandering Albatrosses is the very small proportion (usually <1%) of successful Greyheaded Albatrosses which attempt breeding the next year. It has long been evident that successful Wandering

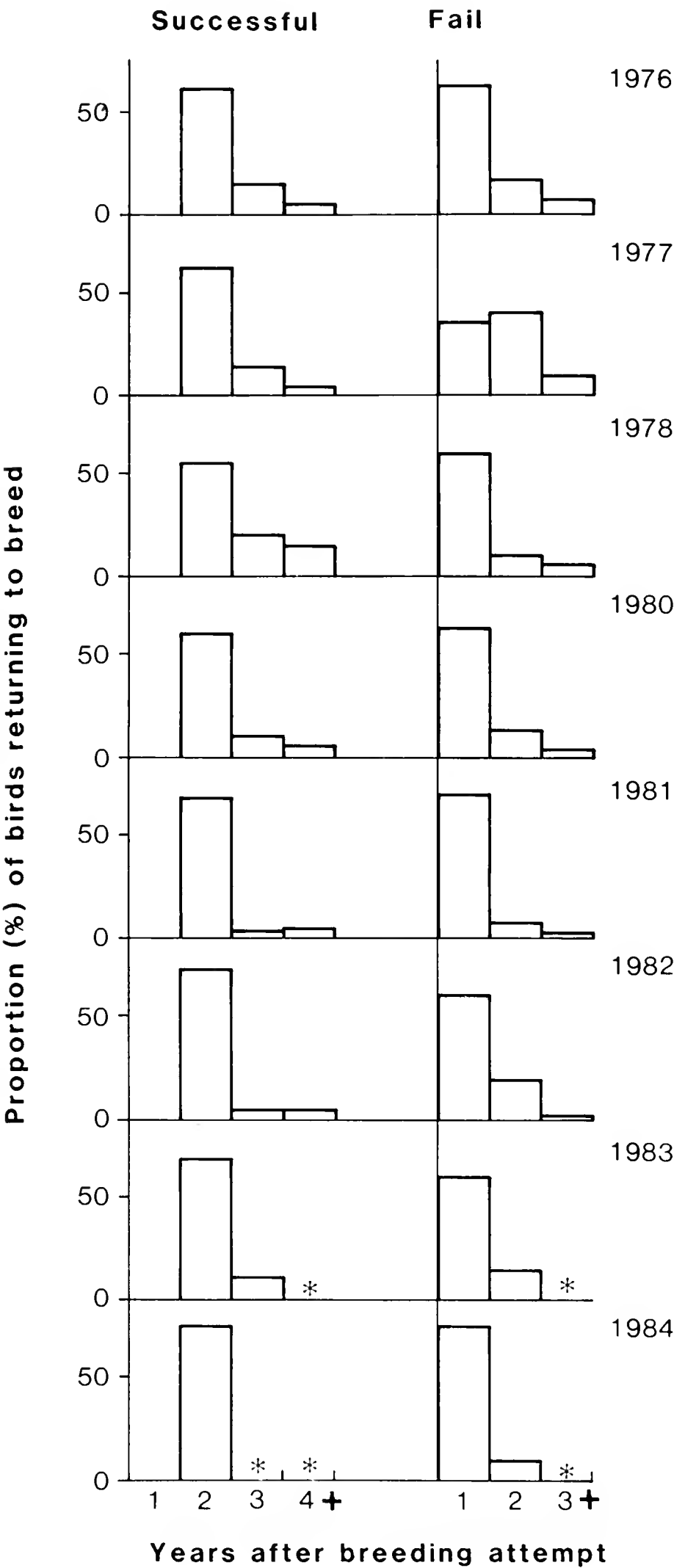


FIGURE 7 - Annual variation in proportion of South Georgia Wandering Albatrosses returning to breed in subsequent years after success and failure in rearing a chick. Asterisk indicates data incomplete.

Albatrosses, with an incubation and chick-rearing period totalling 356 days, cannot breed in successive years (Tickell 1968); interest therefore centres on the nature of the mechanism precluding breeding in successful birds. With the mollymawks, however, incubation plus chick-rearing and the total breeding-attendance period in Grey-headed Albatrosses lasts only 29 and 39 days longer, respectively, than in Black-browed Albatrosses. The small magnitude of these differences raises more fundamental questions about the control and consequences of breeding frequency.

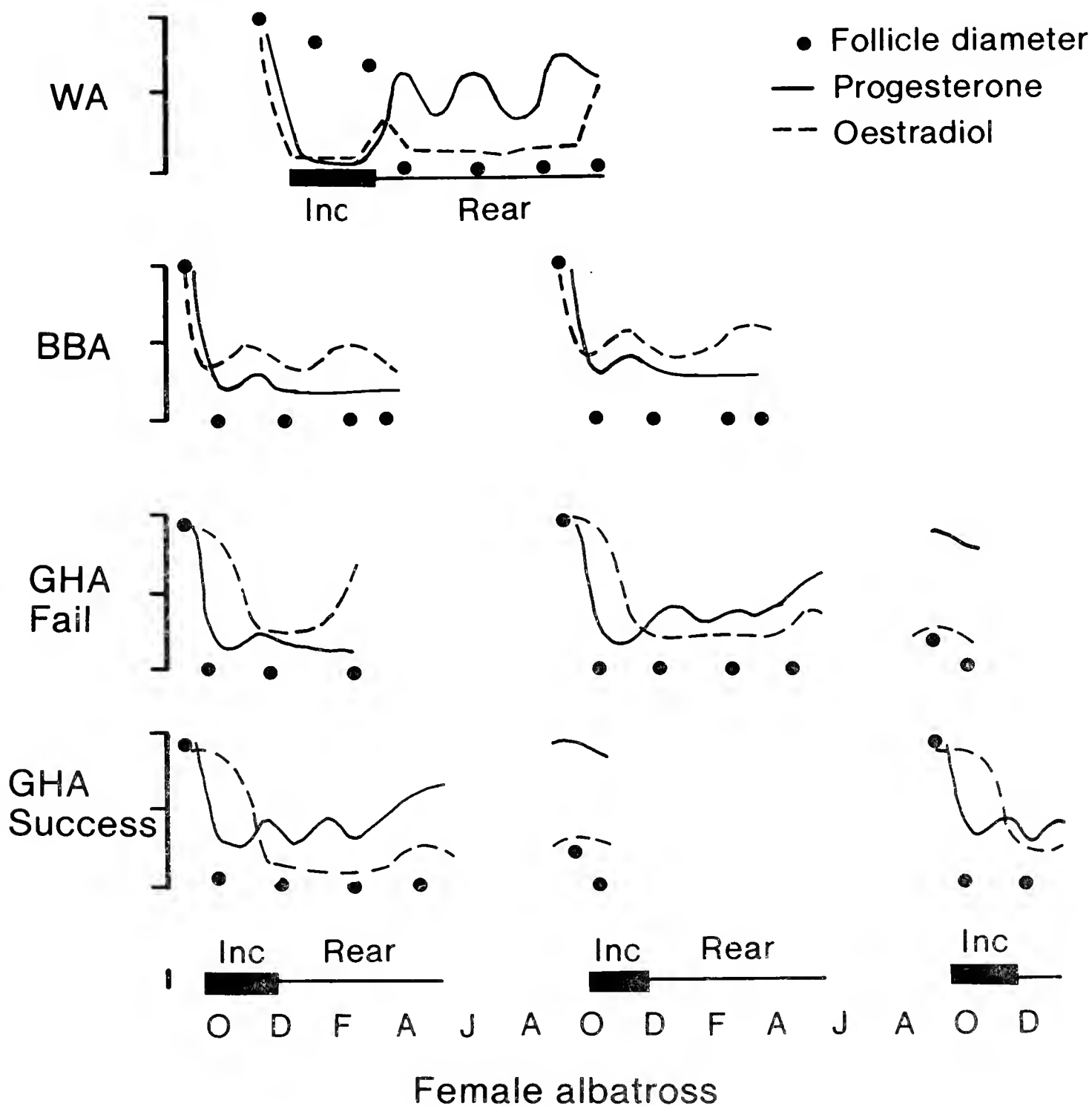


FIGURE 8 - Diagrammatic representation of gonad (follicle diameter) and hormone (concentrations of circulating progesterone and oestradiol) status in female Wandering (WA), Black-browed (BBA) and Grey-headed (GHA) Albatrosses throughout incubation (Inc) and chick-rearing (Rear) and, in GHA Success, while attending the breeding colony in a non-breeding year. (Data from Hector et al. 1986a, b, 1990).

Endocrine influences

Hector et al. (1986a,b) showed that male Wandering, Black-browed and Grey-headed Albatrosses all have annual gonadal and hormone cycles. Successful female Wandering Albatrosses show completely undeveloped follicles throughout chick-rearing and an associated syndrome of relatively high progesterone and low oestradiol levels,

though the latter appear to increase significantly towards the end of chick-rearing (Figure 8). Neither successful nor failed birds reappear until the next breeding attempt, so the stage at which any hormone or gonad development occurs is unknown. Female Black-browed Albatrosses have annual gonadal and hormone cycles irrespective of whether they were successful or not in rearing chicks; they show relatively high oestradiol and low progesterone concentrations during chick-rearing.

When female Grey-headed Albatrosses which failed to rear a chick reappear to breed the next season, in follicle development and hormone profile they exactly resemble Black-browed Albatrosses. If they are then successful in rearing a chick, the circulating progesterone concentration increases sharply late in the rearing season (Figure 8). Of these birds, those that return during the next breeding season (about 40% of the population) show little if any follicular development and high concentrations of circulating progesterone and low concentrations of oestradiol. None of these birds breeds. The key difference between the ability to breed or not in female Grey-headed Albatrosses seems to be correlated with the relative concentrations of oestradiol and progesterone late in chick-rearing - and possibly into the non-breeding season. This is a situation reminiscent of - or even analogous to - that operating in the development of sexual maturity.

This discovery led to two immediate questions. First, why should such a mechanism be developed in Grey-headed and not Black-browed Albatrosses? Second, how can a few Grey-headed Albatrosses breed in the year after a successful season? The answer to these questions requires consideration of the ecological and behavioural context of the physiological mechanisms.

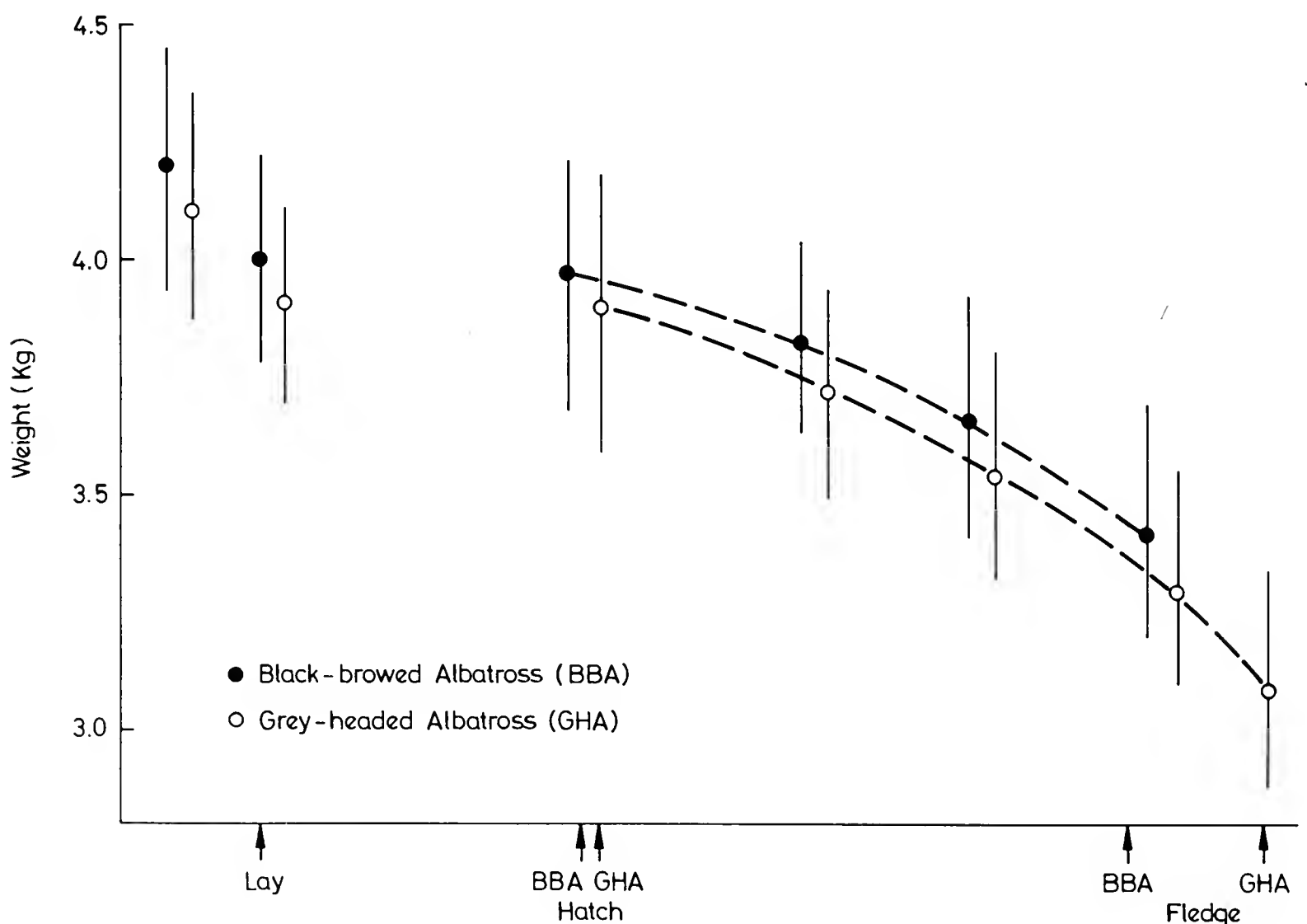


FIGURE 9 - Weights of breeding Black-browed and Grey-headed Albatrosses at South Georgia at different stages of the breeding cycle. (Data from Prince et al. 1981 and unpublished).

Behavioural and ecological influences

The endocrine data indicate that significant physiological events occur at the beginning and end of the breeding season and cycle; these are presumably linked to behavioural and ecological events at similar times. The principal evidence available from such periods concerns change in condition (as indicated by body weight) during breeding and the timing of behaviour around the egg-laying period.

Breeding Black-browed and Grey-headed Albatrosses essentially maintain weight during the period from egg-laying to hatching but lose weight throughout the chick-rearing period (Figure 9). Because successful Grey-headed Albatrosses lose weight for nearly one month longer than Black-browed Albatrosses, by the time the chick fledges they have lost 60% more weight (800g vs 500g). Thus Black-browed Albatrosses have 20% more time to regain a much smaller proportionate weight loss (13% vs 20%), compared to Grey-headed Albatrosses.

It is not surprising, therefore, that Grey-headed Albatrosses should experience greater difficulties than Black-browed Albatrosses in returning to breeding condition in time for the next season. Or that females, needing also to acquire additional energy and reserves for egg formation should be particularly affected. What is perhaps surprising is that the situation is not one in which those birds which can regain breeding condition breed and those which cannot do not. Instead, Grey-headed Albatross females successful in rearing chicks are apparently prevented from even attempting to breed through hormonal suppression of vitellogenesis. This suggests that even for those Grey-headed Albatross females in the best condition at the end of a successful breeding attempt, the cost of attempting to breed in five months time is sufficiently prohibitive for physiological mechanisms to have evolved to prevent it. For birds which fail, however, this block apparently does not exist and female condition in the following September/October presumably determines which birds actually attempt to breed. It should be noted that only 54% of pairs actually breed in the next year with 24% delaying their next attempt for one further complete year (Table 2).

There are, however, no equivalent physiological constraints on male Grey-headed Albatrosses. Nevertheless, almost all males remain faithful to their previous partner and do not breed in the year following one in which they rear a chick. The basis of this seems likely to relate to a combination of factors. First, physiological difficulty in regaining condition quickly enough to breed five months after successfully rearing a chick. Thus only 54% of failed birds manage to breed the next year; furthermore only 40% of successful males attend the colony and only a small proportion of these do so early enough to breed. Second, advantages deriving from continuing to breed with an existing familiar and presumably compatible partner.

There are, however, two interesting features of the behaviour of Grey-headed Albatrosses in their year 'off'. First, the fact that a substantial proportion of birds visit the colony in this year. What is the purpose of this? It cannot be in order to make an extra breeding attempt (but see below) because all females are reproductively quiescent (see above). It is not in order to defend nest sites against incoming breeders because birds arrive too late to do this (Figure 10). The more likely explanations involve renewal of pair bonds and reaffirmation that both partners are still alive. The advantages of doing this might relate on the one hand to improved breeding performance for pairs which meet during the year off and, on the other hand, in cases where only one member of the pair turns up, to receiving advance warning of the possible need to start the

potentially time-consuming task of seeking a new partner. Evidence for improved performance is slight; there are stronger indications of enhanced speed of re-pairing for birds whose partner fails to appear in the year off.

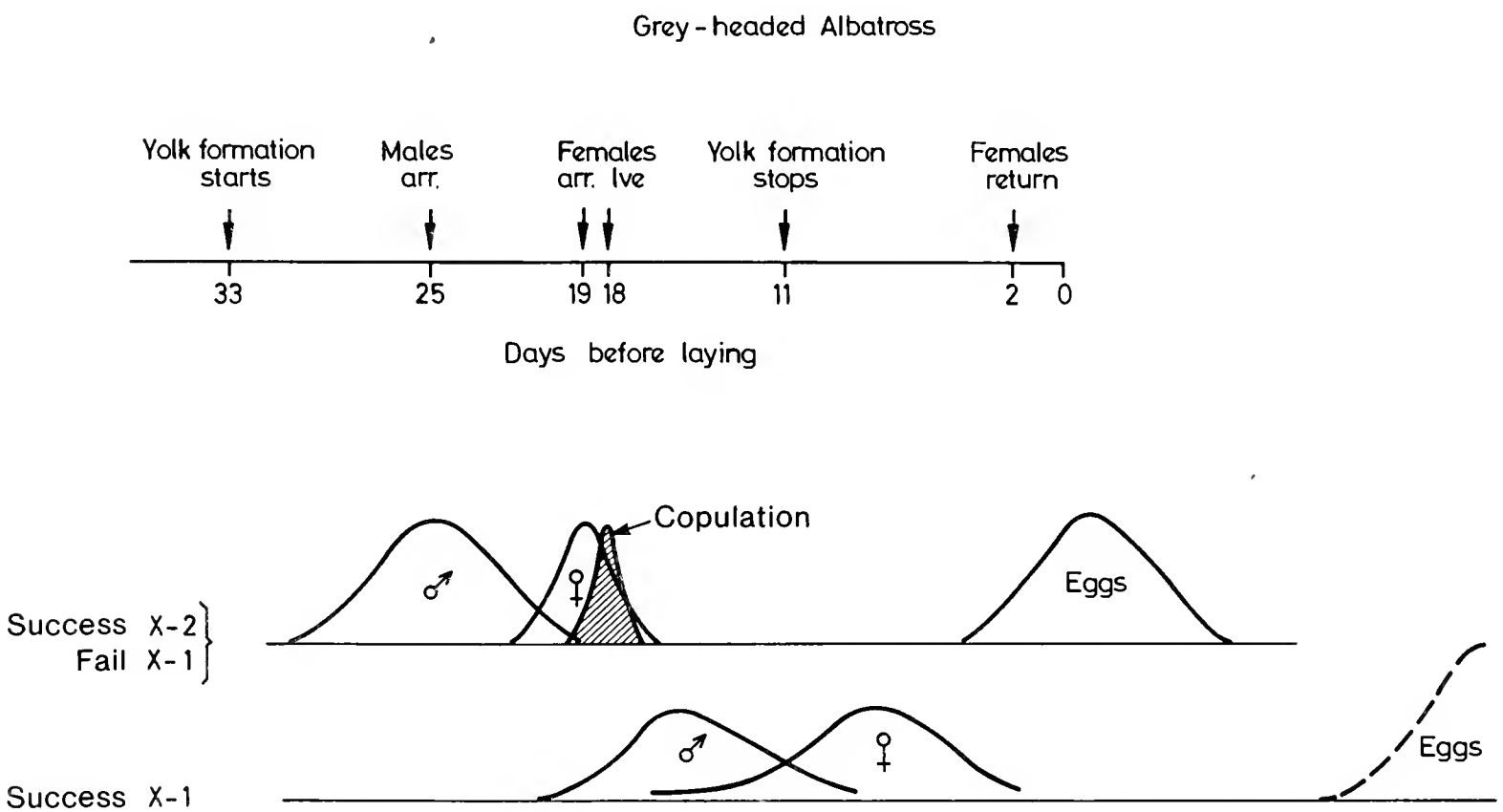


FIGURE 10 - Timing of events at a Grey-headed Albatross breeding colony in the period prior to egg-laying. (Data from Astheimer et al. 1985 and Prince unpublished).

Second, the very small proportion of birds which breed immediately after a successful year (Table 2) comprises only the males from established pairings plus new female partners. This is made possible because males which were successful the previous year arrive significantly earlier than their partners (Figure 10) and overlap with the arrival of established breeding and last time non-breeding females, some of whom will discover that their partners have not turned up. Unless the males' existing partner has disappeared, these pairings rarely last for more than one breeding season, the previous partnership being re-established at the next breeding attempt. The extra breeding attempt by these established males is as successful, on average, as those of any other first time breeder - i.e. slightly, but not significantly less than those by established breeding pairs (see later). We have insufficient data to determine if there is a cost (in terms of reduced survival) to the extra breeding attempt but the advantage gained from this tactic seems small - except in the context of rapid acquisition of a new female partner in a population where competition for females exists.

Within species, assessment of the relationship between breeding frequency and survival requires much more data over complete reproductive lifetimes than we have available currently. However the substantial interspecies difference in mean annual survival between Black-browed Albatross (92%) and Grey-headed Albatross (95%) is consistent with an inverse relationship between breeding frequency and survival (Prince 1980, Croxall 1982, Weimerskirch et al. 1987).

BREEDING SUCCESS

Breeding performance is obviously intimately related to attributes of the individual (e.g. inherent quality, acquired proficiency) but, especially in seabirds which are long-lived and monogamous, also involves a partnership effect (e.g. familiarity, compatibility and the causes and consequences of divorce). There are, as yet, relatively few data on these topics for albatrosses; this section summarises some preliminary findings in relation to the results of studies of other seabird species.

Long-term studies of seabirds have contributed significantly to the body of data on birds indicating that reproductive performance (almost invariably expressed in terms of breeding success) increases with breeding experience. In general, success increases through the first few years of reproduction, then levels off; subsequently there may or may not be a detectable decrease in the performance of the oldest birds. Improving performance is usually attributed to one or more of:

- a) Increasing experience of breeding;
- b) Increasing general competence (e.g. of feeding, avoiding predation, etc);
- c) Increasing reproductive effort to compensate for decreasing survival;
- d) Differential survival, favouring higher quality individuals.

Nearly all seabird studies provide support for the roles of experience and competence (e.g. Thomas & Coulson 1988, Ollason & Dunnet 1988, Reid 1988, Pugesek 1984, Sydeman et al. 1991) but relatively few have been able to distinguish between the two and show that both operate (Nur 1984, Wooller et al. 1990). Although survival rates of many species decline with age and/or experience, the residual reproductive value hypothesis requires increased reproductive effort and success in older birds. The few studies adequately detailed to examine this have not supported the hypothesis (Reid 1988, Sydeman et al. 1991).

Several studies (e.g. Coulson & Porter 1985, Bradley et al. 1989, Sydeman et al. 1991) have shown that long-lived individuals were more productive at some or all stages of their adult life i.e. that quality-related differentials exist. A few studies (e.g. Coulson 1966, Mills 1973, Bradley et al. 1990) have shown that breeding success increases with increasing pair-bond duration, independent of increased overall breeding experience. Divorces are often preceded by a higher than average failure rate (e.g. Richdale 1957, Mills 1973, Nelson 1978, Reilly & Cullen 1981, Shaw 1986, Ollason & Dunnet 1988, Bradley et al. 1990). New pairings frequently experience reduced breeding success initially (Coulson 1966, Mills 1973, Davis 1976, Brooke 1978, Ollason & Dunnet 1988, Bradley et al. 1990), though this rapidly improves if the pair stays together.

If Wandering Albatrosses are typical, albatrosses may be most unusual amongst seabirds in that significant advantages of increasing experience and competence are barely detectable even when comparing birds breeding for the first time with birds of many years breeding experience. Thus for Wandering Albatrosses, first-time breeders are not significantly less successful than more experienced birds in their likelihood of raising a chick to fledge, although differences in hatching success, chiefly because of poor co-ordination of shift routine between the partners, are nearly significant (J P Croxall unpublished data). Lequette & Weimerskirch (1990) found that first time breeders were slightly less efficient at feeding their chicks (in terms of rate of delivery of

meals) than more experienced birds but that this did not persist beyond the early stage of chick-rearing. Thus chick growth rates and ages and weights of fledging was similar in all categories of experienced and inexperienced birds. These findings would support suggestions (e.g. Lequette & Weimerskirch 1990) that when albatrosses first breed they have attained essentially the same foraging competence as experienced breeders.

However, such a conclusion raises some important questions, including whether the effect might simply be characteristic of Wandering Albatrosses and reflect unusually favourable circumstances (e.g. of food supply) while they are rearing chicks.

First, the Wandering Albatross has one of the most consistently high levels of breeding success amongst seabirds (Weimerskirch & Jouventin 1987, Croxall et al. 1988). At South Georgia this ranges from 52% to 73% (mean 64%) over 15 years, whereas other albatrosses show lower and more variable breeding success (Weimerskirch et al. 1986, Croxall et al. 1988), some of which might relate to breeding experience. Clearly the situation in other species of albatross needs to be investigated.

Second, other Procellariiformes which show a similar degree of deferred sexual maturity also show improved reproductive success with greater breeding experience. Thus in the Northern Fulmar *Fulmarus glacialis*, in which the modal age of first breeding in males and females was eight and 12 years respectively, breeding success in both sexes improved until about their tenth breeding year, and thereafter remained approximately constant (Ollason & Dunnet 1988). In the similar Antarctic Fulmar *F. glacialisoides*, breeding success increased significantly with the first three years of breeding experience but did not change significantly thereafter (Weimerskirch 1990). Other Procellariiformes also show clear increases in reproductive success with breeding experience (e.g. Short-tailed Shearwater *Puffinus tenuirostris* (Wooller et al. 1990); Manx Shearwater *Puffinus puffinus* (Brooke 1990)) but these species breed at younger ages – modal age for *P. tenuirostris* is seven years (Bradley et al. 1989) – giving the possibility that acquisition of foraging competence might not be complete before birds start breeding.

Third, it is possible that, in rearing a chick successfully, inexperienced birds suffer a greater cost, (e.g. through working harder and finishing breeding in poorer condition) in terms of subsequently reduced survival or longer intervals between successive breeding attempts, than experienced birds. There is some indication from survival rate (though not from breeding frequency) that this might be so for Wandering Albatrosses (Croxall 1982). Such effects, however, should be more noticeable still in albatross species which breed annually and hence do not have a complete year to recover after a successful breeding season.

The hypothesis that very long-lived species with long-deferred sexual maturity delay breeding until they are fully competent foragers, in contrast to shorter-lived species in which breeding proceeds simultaneously with finishing acquiring foraging competence, requires considerable further study. However it is clear that analysis of the relative roles of inherent quality, acquired proficiency and partner suitability and quality in contributing to reproductive success will require consideration of events and processes prior to the start of breeding. Few such data are currently available, even for comprehensively studied species.

SURVIVAL

For most seabirds longevity is the single most important contributor to lifetime productivity. The significance and relationships of many of the traits and adaptations discussed above can only be adequately assessed in the light of information on their effects on survival and/or on the relationship between longevity and reproductive success. There are two particular problems in doing this with albatrosses.

First, no study of sufficient scope has been conducted for long enough to have data on lifetime reproductive success for even one complete cohort of birds. Therefore most of the topics needing investigating, e.g. the balance of advantage and disadvantage (in terms of productivity and survival) between birds which breed at the youngest possible age and those which delay breeding even longer, cannot yet be studied.

Second, the factors influencing survival of albatrosses (and, indeed, many other seabird species) may have changed drastically in recent decades. Thus for the South Georgia population of Wandering Albatrosses, mean annual survival of juveniles has decreased by 6% (from 90% to 84%) between the 1960s cohorts recruiting in the early 1970s and the 1970s cohorts recruiting in the early 1980s (Table 3). Similarly, mean annual survival of adults decreased by 2-3% (from 96% to 93-94%) from values recorded in the 1960s to those current through the late 1970s and early 1980s (Table 4). These are major changes given the natural demography of albatross populations and may have been even greater for the same species at the Crozet Islands (Weimerskirch & Jouventin 1987) where adult survival averaged 92% and only 26% of juveniles survived to age 5 years (cf. 49% at South Georgia).

TABLE 3 - Mean annual survival of juvenile Wandering Albatrosses at South Georgia, comparing cohorts in the 1960s with those in the 1970s. Sexes combined; based on data in Croxall et al. (1990)

Year	Age (years) surviving to	Ringed	Retrapped	Mean annual survival
1962	9	400	174	0.912
1963	8	1000	399	0.892
Mean				0.896
1972	5	368	143	0.828
1973	5	75	27	0.815
1975	5	854	389	0.854
1976	5	847	337	0.832
1977	5	806	406	0.872
1978	5	871	462	0.881
1980	5	743	342	0.856
Mean				0.854
1972 - 1980	8	4564	1082	0.835

TABLE 4 - Mean annual survival of adult Wandering Albatrosses at South Georgia. Based on data in Croxall et al. (1990).

Cohort	Years	Survival (%)		
		Male	Female	Combined
1958	1976-84	95.4	92.1	93.7
1962	1976-84	94.3	92.6	93.5
1963	1976-84	95.5	93.3	94.4
1958-63	1976-84	94.8	93.1	94.0
Study area	1961-63			95.7
Study area	1976-84			93.2

All the evidence (e.g. Croxall & Prince 1990, Brothers 1991) suggests that the main causes of these changes in survival were catches of albatrosses associated with tuna long-line fisheries, which developed in the 1970s. The fishery-related mortality was not random across sexes and age classes. Females are potentially at greater risk because of their more northerly at sea distribution (Weimerskirch & Jouventin 1987), taking them into the zone of the tuna fisheries. The reality of this effect is confirmed by analysis of ringing recoveries (Croxaall & Prince 1990), movements of satellite tracked birds (P A Prince unpublished data) and by the significantly lower survival rates of females (Table 4; Croxall et al. 1990). In addition, adults seem to be more susceptible than juveniles (Croxaall & Prince 1990), possibly because they are socially dominant to juveniles in the melees around fishing boats.

However, birds of all sexes and ages were killed and in such numbers as to represent at least 50% of the total annual mortality of each sex and age class (Croxaall et al. 1990). The imposition of such a level of mortality likely to be unrelated (or related in ways very different from previously) to characteristics like bird condition, quality, previous breeding experience etc, is likely severely to compromise attempts to relate longevity and reproductive success to reproductive tactics and strategies. Failure to derive significant relationships in regard to survival (e.g. the lack of age-related survival in the Wandering Albatross) may well not be typical of natural populations but simply reflect the results of recent artificial influences.

CONCLUSIONS

Many aspects of our studies of albatross biology and ecology have produced similar results to the often much longer term and more extensive studies of other seabird species. However, there are a number of unique results, some of which may prove to be characteristic only of albatrosses but others of which may have much broader applicability.

One such feature is that there may be significant differences between the sexes in physiological and related behavioural and ecological adaptations. Thus in the Wandering Albatross one essential difference between the sexes in physiological terms is that males are sexually mature at an earlier age than females. This presumably reflects the much greater magnitude (in terms of time spent in duties ashore) of the change between non-breeding and breeding status for females than for males and the

additional costs of egg formation in females. The costs of breeding too early in females are presumably sufficiently great for a physiological mechanism to have evolved to prevent premature reproduction.

In behavioural terms the most surprising finding was that despite the relatively highly evolved displays and the distinct sexual dimorphism in size and plumage in Wandering Albatrosses the principal male signal acted on by females appeared to relate to the duration and/or frequency of attendance ashore. In spending time ashore males are advertising their ability to cope with the demands of fasting - the key adaptation required once they start breeding in order to cope with the long incubation shifts. Female commitment to life ashore is significantly less than males, so in both endocrine and behavioural terms females appear to be protected from sustaining undue stress.

Because Black-browed and Grey-headed Albatrosses are the same size and have very similar timing and rather similar duration of breeding events, yet breed annually and biennially respectively, they are uniquely suitable for investigating control of breeding frequency.

Even in a species whose sexes are of very similar size and structure, there may be significantly different physiological influences on the two sexes. Thus in the Grey-headed Albatross an endocrine-mediated mechanism prevents females, but not males, from breeding immediately following success in chick-rearing. Bienniality in males seems to be maintained by a combination of physiological difficulty in regaining condition and advantages of continuing reproduction with a familiar, experienced and presumably compatible partner.

The absence of an endocrine constraint to breeding frequency in males may help them, in circumstances of actual or potential mate loss, to start re-pairing as soon as possible. This is desirable because there are usually fewer unpaired adult females than males. Informing their partners of their continued survival is presumably one reason why substantial numbers of Grey-headed Albatrosses of both sexes try to return in their year off.

Because albatrosses are essentially pelagic throughout their inter-breeding period, evidence for the proximate influence of condition on breeding ability and frequency will be very difficult to acquire. However, in addition to regaining body condition following breeding, albatrosses also need to undertake moult (no species moults during its breeding season). In the Wandering Albatross, Weimerskirch (in press) has demonstrated inverse relationships between body weight and moult (in males but not females) and direct relationships between time between breeding attempts and moult (in females but not in males), which suggest that the energy costs of moult may not be insignificant and that the two sexes may experience different constraints in this regard.

Although a strong interspecies correlation exists between breeding frequency and survival there are so far insufficient data to demonstrate this intraspecifically. Breeding success in albatrosses appears to be much less influenced by experience than in other seabirds - perhaps because they have acquired sufficient experience during the lengthy periods of immaturity and pair formation prior to starting breeding. Much more

work is needed on this topic in albatrosses and seabirds generally. Except for the Wandering Albatross, which has shown consistently high breeding success over the last 15 years, variation in breeding success may relate significantly to the particular years in which breeding is attempted and especially to the avoidance of years of poor breeding success for the whole population. At South Georgia such years occur relatively frequently (Croxall et al. 1988), although they are often associated with smaller breeding populations and higher indices of deferred breeding than usual (Croxall & Rothery 1991). In any case the role of breeding frequency in determining overall productivity will be much less significant than the influence of longevity. Albatrosses live so long that data on lifetime reproductive success are very slow to accumulate and it is impossible at present to assess the consequence of reproductive tactics and strategies. However the magnitude of changes in Wandering Albatross survival over recent decades, due principally to human fishing activities, raises the strong possibility that mortality from these sources may prevent detection of the subtler effects of individual differences in reproductive adaptations.

There is also the broader concern, noted by Croxall & Rothery (1991), that because human influences include direct predation, competition for common resources, mortality through introduced animals, destruction of breeding habitat and pollution of feeding habitat, few, if any, data on seabird populations come from sites and systems unperturbed by man. There is a real danger that the responses of populations of seabirds, especially those species with long generation times and low productivities, may no longer be to a range of relatively constant and predictable natural factors but instead, so far as they are able, to a variety of rapidly changing and unpredictable constraints imposed through human interference.

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SYMPOSIUM 1

**BIOGEOGRAPHY AND SPECIATION
IN NEOTROPICAL BIRDS**

Conveners K-L. SCHUCHMANN and F. VUILLEUMIER

SYMPOSIUM 1

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INTRODUCTORY REMARKS: BIOGEOGRAPHY AND SPECIATION IN NEOTROPICAL BIRDS

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The Neotropics are inhabited by the most diverse avifauna in the world. Roughly 3300 bird species have been documented, among them only 180 migrants from North America. This contrasts with about 1600 resident species within the Afrotropics, 961 in the Oriental Region and 906 in Australasia. Compared to the ornithofauna of tropical Africa to Australia, the Neotropical avifauna is taxonomically very different and, due to a long-lasting geological isolation, comprises a high percentage of endemic bird families (30%). The high degree of taxonomic differentiation is illustrated by the species/family ratio, which is 33.9 for South America against 22.4 for Africa and 14.6 for Australia.

During the past two decades Neotropical ornithology has benefitted greatly from new publications, especially regional bird lists, field guides and handbooks. This has improved the active research participation of amateur ornithologists and resulted in a cooperation with professionals similar to that in northern countries. Today, a wealth of new data has become available including information on abundance of birds in space and time, on geographical variation and ecological requirements of species inhabiting a given region. With this new knowledge as background numerous analytical studies on zoogeography and speciation have been carried out.

The following two questions will form the framework of our symposium: What are the historical roots of the present-day distribution of neotropical birds, and how can we explain speciation patterns?

Since Darwin and Moritz Wagner, the biogeographical analysis of distribution has helped to identify the degree and patterns of isolation which are prerequisites to genetical differentiation of populations at the species level, during the process of allopatric speciation. Parapatric speciation is caused by genetical differentiation of continuously distributed populations influenced by ecological gradients, sympatric speciation by chromosome and other local changes within a population. However, parapatric and sympatric differentiation in vertebrates, especially in birds, probably had minor impacts on speciation. Geographical isolation of populations seems decisive for species differentiation in continental faunas. It is supposed to have been caused by two processes: fragmentation of formerly continuous areas (vicariance), and transgression of barriers by groups of individuals (dispersal, founder populations). These processes were probably influenced heavily by climatic effects.

Two hypotheses are presently being discussed to explain the mosaic-like distribution patterns and the speciation events of Amazonian lowland-forest superspecies: the refuge hypothesis and the riverine hypothesis. The refuge model is based on

cyclical climatic fluctuations causing expansions and contractions of dry to humid terra-firme forest and of non-forest habitats, especially during Quaternary and Tertiary, but not restricted to these epochs. The riverine model, on the other hand, assumes the fragmentation of bird ranges during the development of the extensive Amazonian river system as a consequence of the uplifting of the Andes.

For montane species similar hypotheses would be the refuge model and a mountain-range isolation model. Both of these would be modified by orogenic processes.

The speciation events as a consequence of climatic fluctuations are theoretically convincing, but we still lack conclusive evidence to support the refuge idea. Moreover, we rarely know whether speciation events were caused by recent climatic cycles, earlier cycles, or both. As to unsolved problems connected with the riverine (or mountain-range) model, we have to deal with the origins of those lowland forest birds to which rivers hardly represent barriers and with those birds which have continuous distributions in the headwater regions where the rivers cease to be barriers. Probably, distribution and speciation result from both isolation types: rivers or mountain ranges and habitat refuges. With further biological and geological information, it may be possible to assess the general validity of these models.

For the near future our work on biogeography and speciation of Neotropical birds will profit greatly if we continue our studies on phylogenetic affinities within species groups by cladistic methods, establishing phylograms based on geology and comparing them with cladograms based upon anatomical, behavioural, and biochemical information. Additionally, our studies of geographical variation would be facilitated if more computer generated contour map studies of character scores and measurements would become available (Haffer and Fitzpatrick method). All our challenging projects can only be achieved if we can continue responsible collecting of specimens all over Central and South America. International collaboration projects would be very useful.

A major objective of present activities of amateurs and professionals is to prepare an atlas of speciation in Neotropical birds. The first step needed to realize this ambitious plan is to publish detailed range maps of birds from those states and countries where the avifauna is known in great detail. The gazetteers of Latin America edited by R. Paynter and collaborators will be invaluable. Computerization of specimen collections and of records in the literature is highly desirable, especially lists of locations of type specimens as we discover unexpected sibling species or specific differences between birds previously thought to be subspecies. A variety of museum, field and laboratory studies will be needed and should receive support.

NEOTROPICAL AVIAN DIVERSITY AND RIVERINE BARRIERS

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ABSTRACT. The high frequency with which rivers delimit phenotypically differentiated bird taxa (species, subspecies) is unique to Amazonia. The riverine barrier hypothesis (an alternative to the Pleistocene refugia hypothesis) posits that the high regional species richness in Amazonia resulted from the development of the riverine system. These hypotheses are evaluated in the light of the knowledge of patterns of phenotypic and genetic differentiation in birds and the current geological evidence. Predictions are developed by which to test these hypotheses, gaps in our current knowledge are profiled, and specific research programs are recommended.

Keywords: riverine barriers, refugia, bird diversity, Amazonia.

INTRODUCTION

For birds, the Amazon basin (South America) has the highest alpha (single-point) and gamma (regional) species diversity (Amadon 1973). Hypotheses to explain this diversity are ecological and historical. Ecological hypotheses address the causes of single-point diversity, and in part regional. To explain fully regional diversity, historical hypotheses have been offered.

Of the historical hypotheses advanced, the Pleistocene refugia hypothesis (Haffer 1969) is widely accepted (Prance 1982). It states that regional diversity is attributable to the periodic fragmentation and coalescence of the forest during Pleistocene climatic fluctuations. The isolation of forest fragments (refugia) is the major promoter of speciation, and rivers only constitute a partial barrier to species' re-expansion following climatic amelioration (Haffer 1974).

Another historical hypothesis, suggested by the congruence of many birds' ranges with rivers, is that the formation of the Amazonian river system after the uplift of the Andes induced speciation in forest-dwelling birds by fragmenting their ranges and prohibiting gene flow. Under this hypothesis, regional diversity derives from riverine barriers serving as a vicariant mechanism interrupting gene flow (Sick 1967).

Although these hypotheses are not mutually exclusive, there is a profound difference between them: the existence of the vicariant agent for the Pleistocene refugia hypothesis (isolated forest refuges) is inferred, while the vicariant agent for the riverine barrier hypothesis (riverine system) is known to exist. As discussed herein, recent geological and biochemical systematic evidence have challenged the existence of Amazonian refugia. If refugia did not exist, then our understanding of speciation mechanisms in Amazonia must be re-evaluated.

In this paper, I summarize some evidence bearing on the two hypotheses, develop predictions to test them, identify gaps in our knowledge, and offer research programs to improve our understanding of regional species diversity in Amazonia. Finally, I touch on the conservation implications of this issue.

GEOLOGICAL EVIDENCE

The majority of geomorphological, palynological, and paleoclimatological data used to support refugia is derived from sites in the Andes or peripheral to forested Amazonia (Prance 1982). Such evidence from within the basin is equivocal (Salo 1987, Colinvaux 1989). One study directly challenges the refugia hypothesis by interpreting pollen and megafossil remains from the western edge of the putative Napo refugium as harbouring montane vegetation, not lowland tropical forest, during a mid-Wisconsin interstade (Colinvaux 1987).

The crux of the argument regarding the effects of glacially-induced climatic alteration is which effect—reduction of precipitation and/or reduction of temperature—most strongly affected the vegetation. (The geological timing of these events is a separate problem discussed under prediction 2.) Under the refugia hypothesis, substantial aridity caused the forest to be replaced by savanna, except in mesic areas (Haffer 1969). An alternative is that the reduction of precipitation was insufficient to fragment the forest; rather, forest vegetation zones contracted under the influence of reduced temperature so that peripheral open habitats expanded and the montane/lowland tropical forest ecotone dropped in elevation (Colinvaux & Liu 1987). Therefore, the central question is whether the Amazonian lowland tropical rain forest fragmented or contracted. Due to the lack of data from within the basin, this question cannot be answered currently. For this reason, current patterns of species distributions are used to infer previous vicariant events.

BIOLOGICAL EVIDENCE

Phenotypic differentiation

The observation that Amazonian rivers delimit the range of many taxa of volant birds is in textbooks (e.g. Wallace 1876, Mayr 1942), general avifaunal works (e.g. Hellmayr 1910, Snethlage 1913), and discussions of specific taxonomic groups (e.g. Todd 1927). Hellmayr (1910) reports that the Madeira River delimits the range of 67 taxa. The lower Amazon river delimits the range of 80 taxa, and three large tributaries of lower Amazonia—Tocantins, Xingu, Tapajoz—delimit 37, 22, and 12 taxa, respectively (Snethlage 1913). Three seasons of field work in the upper Amazon (Iquitos) documented 4 taxa delimited by the lower Napo river and 24 delimited by the wider Amazon river (Capparella 1987). In presenting such tabulations, authors usually differentiate between two categories: 1) taxa which have an opposite bank replacement form, and 2) taxa which do not. In the case of the former it is assumed, but has not been demonstrated, that the two are sister taxa.

Despite these tabulations, a complete published list of the number of taxa delimited by rivers in Amazonia is lacking, although such a list could be compiled from the data utilized by Haffer (1978) and the information in Peters (1934-1987). Problems with such a list stem from the uncertainty regarding the ranges of Amazonian birds (e.g. Parker & Remsen 1987) and the delimitation of taxon limits (e.g. Capparella & Rosenberg in press). Additional collections are needed, particularly in the headwaters, where the breakdown of river-delimited ranges are most likely (e.g. see Bates et al. 1989). One uncertainty in compiling such lists is illustrated by comparing the species collected at three sites within 80 km in contiguous forest along the north bank of the Napo and Amazon rivers (Capparella 1987). Although there is considerable

similarity in species composition and number, some species (e.g. Black-headed Antbird, *Pernostola rufifrons*; all names from Meyer de Schauensee 1970) were collected at only one site. This complicates the determination of rivers delimiting species ranges because a sample at a single trans-river site may not detect the species, even though it is present at other sites on the same bank.

Three kinds of differences, other than sampling error, may explain these among-site changes in understory avifauna: 1) microhabitat availability, 2) seasonal or mobile resources, and 3) bird density. These factors must be evaluated when determining the likelihood that a species is truly absent from a particular region and interpreting such absence as indicative that this species' range is delimited by a river. For example, the Black-headed Antbird absence may be attributable to the first factor. On the other hand, some species appear to be absent even when there is not a clear-cut replacement taxon (e.g. White-plumed Antbird, *Pithys albifrons*, absent south of the Amazon).

Genetic differentiation

Genetic differentiation among river-separated populations of species that do not differ in plumage has been demonstrated using protein electrophoresis. River-congruent genetic differentiation is known in five monomorphic, *terra firme* (not seasonally flooded), forest-understory birds (river given after name; A=Amazon, N=Napo): Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*; Dendrocolaptidae; A, N), Stipple-throated Antwren (*Myrmotherula haematonota*; Formicariidae; A), Blue-crowned Manakin (*Pipra coronata*; Pipridae; A, N), Black-faced Antbird (*Myrmoborus myotherinus*; Formicariidae, A, N), White-plumed Antbird (*Pithys albifrons*; Formicariidae; N) (Capparella 1987, 1988; Hackett & Rosenberg 1990). In addition, genetic differentiation among phenotypically differentiated, river-delimited taxa has been demonstrated for: Long-tailed Hermit (*Phaethornis superciliosus*; Trochilidae, A, F. Gill & J. Gerwin pers. comm.), Blue-crowned Manakin (*Chiroxiphia pareola napensis* and *C. p. regina*; Pipridae, A), Golden-headed/Red-headed Manakin allospecies (*Pipra erythrocephala* and *P. rubrocapilla*; Pipridae; A) (Capparella 1987, 1988). These taxa span a diversity of familial affinities and life history traits sharing only their occurrence in the understory of *terra firme* forest.

I expect the congruence of genetic differentiation with rivers to be a general phenomenon among understory *terra firme* forest birds, although the minimum size-class river that will show this effect is not known. The number of genetically differentiated forms delimited by rivers is clearly greater than that predicted from plumage differences alone, although vocal differences may tell a story akin to allozymes (T. A. Parker III, pers. comm.). Interestingly, the levels of differentiation across the Amazon for four non-phenotypically differentiated birds (Wedge-billed Woodcreeper, Stipple-throated Antwren, Black-faced Antbird and Blue-crowned Manakin) are comparable to the mean value for temperate zone avian species (Capparella 1987, Hackett & Rosenberg 1990).

The examination of patterns of genetic differentiation among Amazonian birds is in its infancy. Unknown at present is if other general classes of birds, especially *terra firme* forest-canopy birds and *varzea* (seasonally flooded) forest-understory birds, will also show genetic differentiation congruent with rivers. The paucity of river-associated phenotypic differentiation in most canopy birds (e.g. Isler & Isler 1987) suggests there may not be river-associated genetic differentiation. If so, this would support the interpretation that neotropical birds inhabiting the dark understory of *terra firme* forest will

not cross light gaps such as rivers (Capparella 1987). Canopy species, occupying the well-lighted top of the forest, may not show such "negative phototaxis". However, the presence of phenotypic differentiation in some canopy groups such as toucans (Ramphastidae) that is only partially congruent with rivers has been offered both in support of Pleistocene refugia (Haffer 1974) and against it (Cracraft & Prumm 1988). The lack of river-associated phenotypic differentiation in most *varzea* birds suggests there may not be river associated genetic differentiation in these species. This suggests that the transitory nature of *varzea* forest requires across-river dispersal or, alternatively, the formation of oxbows by rivers is causing passive dispersal of opposite bank *varzea* forest with the birds. A biochemical systematic approach is needed to characterize genetic differentiation within these bird groups.

THE HYPOTHESES

The riverine barrier hypothesis

The riverine barrier hypothesis is implicit in earlier writings (e.g. Wallace 1876, Hellmayr 1910, Sneath 1913) and was discussed by Sick (1967). It begins with the formation of the Amazonian lowlands due to the rise of the Andes, completed some 2 million years ago, leading to deposition filling in the lake occupying the centre of South America. This permitted the colonization of new land by forest and birds from sources located on the Guianan shields. The rise of the Andes initiated also the formation of the drainage pattern that has become the Amazon riverine system. As these rivers increased in width, they began to fragment the rain forest and the ranges of birds that inhabited them.

The effects of glacially-induced climatic effects on this process are unclear. The following have been proposed: 1) an Amazon river embayment which would widen the lower Amazon and its tributaries (Haffer 1974), 2) lakes and extensive flooding at various times (Campbell & Frailey 1984), and 3) lowering of the montane-lowland forest ecotone deeper into the headwaters (Colinvaux & Liu 1987), thereby preventing gene flow. However, the central tenet in the riverine barrier hypothesis is that the rivers themselves were the primary vicariant mechanism, regardless of possible ancillary processes.

The explanatory power of this or any other vicariant model is its ability to account for a substantial number of bird distributions. The assumption is that a common thread does explain the majority of distributions in Amazonia and that it is not the result of a multiplicity of forces that have operated independently on each taxon. This was the appeal of the Pleistocene refugia model. The appeal of the riverine barrier model is that the agents of vicariance—the rivers—are known to exist while the existence of refugia are as yet only inferred.

Rivers versus refugia

The riverine barrier and Pleistocene refugia hypotheses both state that rivers can serve as barriers, although they differ regarding their effectiveness. The former states that rivers cause differentiation whereas the latter views rivers as limiting the re-expansion of taxa formerly isolated in refugia and/or providing a location (due to reduced gene flow) at which a contact zone between former refugia can stabilize. Although the causes are different, the resultant patterns would be similar so it is difficult to develop

predictions to distinguish between them. Following are four predictions that should permit testing these two hypotheses.

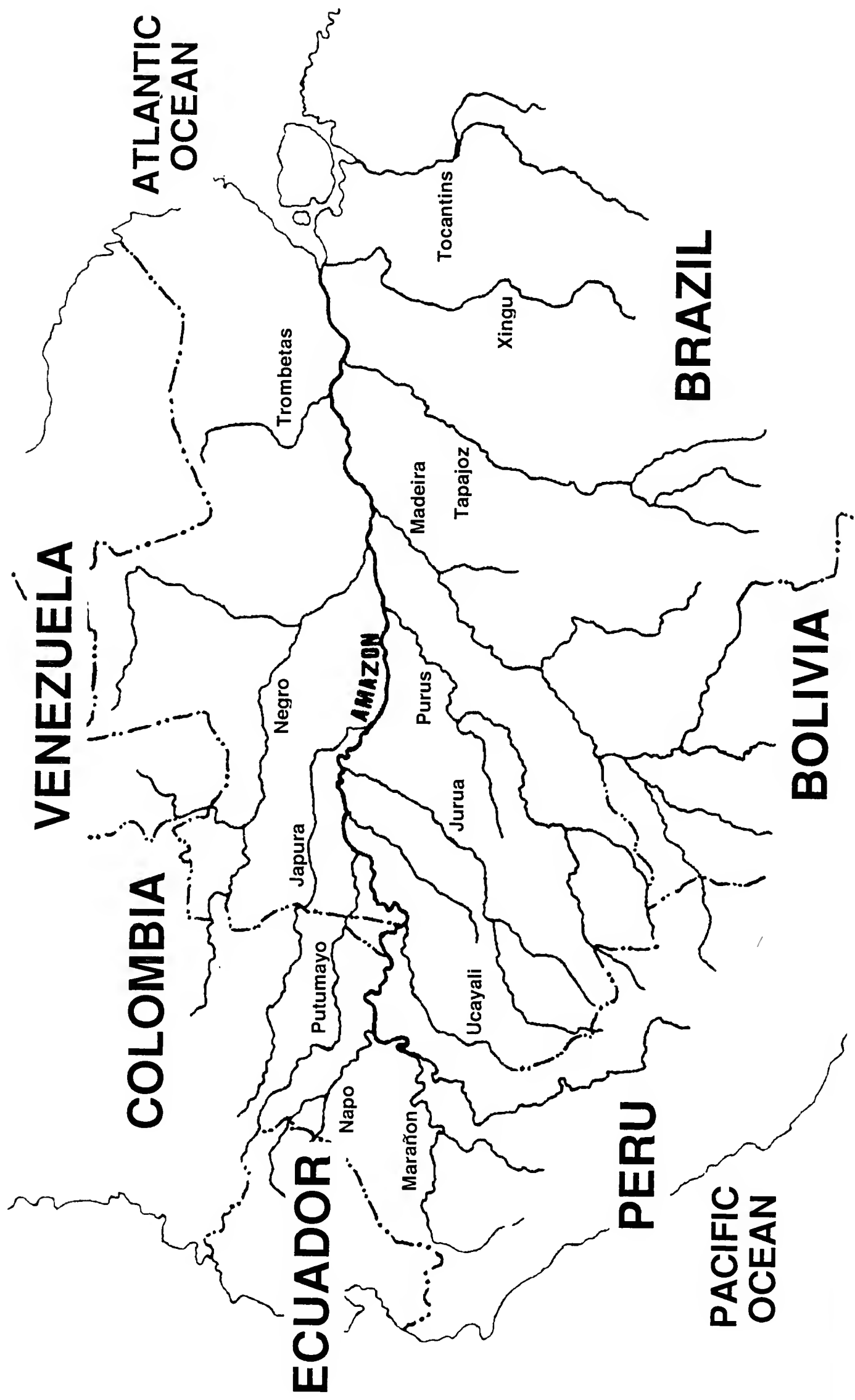
PREDICTION 1. *Terra firme* forest-understory birds, regardless of taxonomic affinity or level of phenotypic differentiation (from none to substantial) will show significant genotypic differentiation across the major rivers of Amazonia when examined by biochemical methods. As described earlier, this has been shown for several species across the Napo and Amazon rivers. Interestingly, the level of differentiation was higher across the Amazon than across the Napo. Whether this is due to the recency of attainment of the present width of the Napo, the occurrence of more frequent oxbowing permitting passive transport, or the capability of headwater crossing remains to be determined. If the latter is the case, one would expect to find clinal variation among samples taken further upstream on both banks. Further sampling of taxa across other rivers is needed to confirm this general pattern and determine what minimum size-class river is associated with genotypic differentiation. Although confirmation of this prediction does not rule out refugia, it appears to obviate the need to postulate refugia for *terra firme* forest-understory birds.

PREDICTION 2. The calibrated genetic distance value (i.e., a time estimate) between sister taxa separated by a river will be clustered around 1-2 million years ago (m.y.a.) under the riverine barrier hypothesis instead of a spread of values over a 6-million-year interval in the refugia hypothesis. The completion of the Andean uplift and concomitant river formation was Late Pliocene-Early Pleistocene (some 2 m.y.a.). The glacially-induced climatic fluctuations affecting South America are now thought to have begun in the Late Tertiary as much as 6 million years ago (Van der Hammen 1985; Van Zinderen Bakker 1986), and this has led to a modification of the original Pleistocene refugia hypothesis (J. Haffer pers. comm.). The onset of refugia now dates to the Late Tertiary and there were pulses of refugia until the last glacial event in the Late Pleistocene. This modification is substantial because a major consequence of the original hypothesis (Haffer 1969) was that regional species diversity in Amazonia dates from the Pleistocene.

The neutral mutation model of the evolution of electrophoretic characters states that they evolve in a roughly time-dependent manner. This theoretically permits the utilization of genetic distances to date divergence events. However, the existence of a proper calibration time remains controversial. Application of one commonly cited value (Gutierrez et al. 1983) to previously described Amazonian taxa reveals that sister taxa of suboscine Amazonian birds are, on average, much older than taxa of temperate zone birds (Hackett & Rosenberg 1990). For trans-Amazon taxa mentioned earlier, the median value of 1.6 m.y.a. supports the prediction of the riverine barrier hypothesis (Capparella 1987, 1988, Hackett & Rosenberg 1990). Further calibrated values are needed to determine if there is a concentration around 2 m.y.a. or a spread of values over a 6-million-year interval.

PREDICTION 3. Allozyme heterozygosity values and mitochondrial DNA clonal diversity values will decrease outward from the core of each refugium. The expansion of the formerly restricted taxa into newly arising forest would involve a stepwise series of founder events. A transect through a putative refugium should reveal a central core of high allozyme heterozygosity/mtDNA clonal diversity with a decrease as one moves away from the core, assuming that the expanding peripheral populations have not reached equilibrium.

FIGURE 1 - Map of Amazonia with rivers between which are 14 interriverine "islands" predicted to contain concentrations of taxa on unique evolutionary trajectories. These faunal units are named: east Trombetas, Negro-Japurá, Japurá-Putumayo, Putumayo-Napo, Napo-Marañón, Marañón-Ucayali, Ucayali-Juruá, Juruá-Purus, Purus-Madeira, Madeira-Tapajoz, Tapajoz-Xingu, Xingu-Tocantins, east Tocantins.



This pattern is not expected under the riverine barrier hypothesis. Unfortunately, such a transect would be logistically difficult.

An interesting variant of prediction 3 involves a consequence of forest re-expansion across rivers. For example, a black-bodied subspecies of the Blue-crowned Manakin is proposed to have originated on the north bank of the Amazon in the Napo refugium. It is now found on the south bank because when the forest re-expanded, the black-bodied subspecies reached and crossed the Amazon. Under this prediction, one expects a difference in diversity of genetic markers in samples of the black-bodied form on both sides of the river. The south bank forms were founders, probably not freely crossing the river, and therefore should show less allozyme heterozygosity and mtDNA clonal diversity. However, if the Amazon river merely bifurcated the two ranges there should be equal amounts on both banks. Similar situations should exist with other taxa and other rivers in Amazonia.

PREDICTION 4. The number of rare alleles will increase outward from the core of the refugium. If the founder populations are still increasing in number, then theoretical models predict an excess of rare alleles in those populations (Maruyama & Fuerst 1984). This prediction also assumes that the peripheral populations have not rebounded to reach an equilibrium. This pattern is not expected under the riverine barrier hypothesis. Large sample sizes and appropriate genetic markers are needed to test this prediction.

Problems with the riverine barrier hypothesis

When examining patterns of phenotypic differentiation in Amazonia two fundamental observations can be used to argue against the riverine barrier hypothesis: 1) the inconsistency of congruence between phenotypic differentiation and rivers, and 2) the existence of suture zones, i.e., congruent contact zones between phenotypically differentiated taxa that occur in the middle of forest unassociated with rivers (Haffer 1987). As discussed earlier, lack of phenotypic differentiation does not mean lack of genetic differentiation. Therefore, it is critical to determine the patterns of genotypic differentiation. The demonstration of extensive genetic differentiation among phenotypically monomorphic, *terra firme*, forest-understory birds separated by rivers suggests that there is no inconsistency in congruence between genetic differentiation and rivers; therefore, the first argument is weakened.

Due to our incomplete knowledge of the distribution of Amazonian birds (e.g. Parker & Remsen 1987) and sampling problems that compromise the thorough inventory at any one site (see phenotypic differentiation section), putative suture zones may be an artifact. If not, then the existence of suture zones not associated with rivers is the strongest evidence for the refugia hypothesis. One way to invoke the riverine barrier hypothesis is to assume a major river course change permitting the contact of formerly river-delimited forms and/or to attribute suture zones to the meeting after re-expansion of forest beyond the headwaters of rivers. While evidence for major river course changes has been presented (Salo et al. 1986), the acceptance of frequent changes in river courses is a problem for the riverine barrier hypothesis because it could lead to the prediction of a homogenization of regional diversity as formerly isolated interriversine areas come into contact (unless sufficient time for differentiation has occurred).

An alternative explanation is suggested by the environmental gradient hypothesis (Endler 1982). Endler proposes that present-day ecogeographic factors permit the development of clinal variation that can lead to parapatric speciation without geographic isolation. Therefore, a suture zone may be an abrupt step in a cline. This assumes that gene flow is not sufficient to overcome the selective influence of the environmental gradient responsible for promoting differentiation. This view challenges the assumption that strong geographic differentiation in birds can only evolve with complete geographic isolation and implies that these avian contact zones are the result of primary, not secondary, introgression.

Recent work on isozyme variation within Amazonian birds in continuous forest has revealed levels of genetic differentiation higher than expected from studies of temperate zone species (Braun & Parker 1985, Capparella 1988). It is therefore possible that the response to an environmental gradient would produce differentiation without allopatry in tropical birds. To determine this it is necessary to effect a transect across a suture zone. Because suture zones are in the middle of forest this is logistically difficult. However, a transect of this type has recently been accomplished across a putative suture zone in southeastern Peru (several Louisiana State University Museum of Natural Science expeditions), and the pattern of genetic differentiation should clarify the reality and significance of suture zones.

CONSERVATION

The distinction between the riverine barrier and refugia hypotheses is important from a conservation perspective. One approach to identifying forest areas for reserves involves the determination of putative refugia because these are considered to be the source areas for present-day biotic diversity (Wetterberg 1976, Gentry 1986). The evidence presented earlier casts doubt on the necessity for postulating refugia when potential vicariant elements—rivers—are known to be present. If putative refugia are not the centres of biotic diversity, then the refugia method of identifying areas for preserves is not valid. If rivers are the chief agents enhancing regional species diversity, then only thorough inventory of many sites within the Amazon basin will permit the identification of regions of unique biotic diversity for preservation.

Using the analogy of “an archipelago of islands” (Snethlage 1913), coupled with current knowledge of patterns of avian differentiation, it is possible to identify 14 “islands” of *terra firme* habitats bounded by rivers (Figure 1). These interriverine areas should contain entities (specifically, *terra firme* forest-understory birds) on unique evolutionary trajectories (*sensu* Cracraft 1983), so-called “evolutionary significant units” which should be the objects of conservation management (Barrowclough & Flesness in press). Therefore, these 14 faunal units should be targeted for reserves to maximize the preservation of Amazonian biotic diversity.

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DISJUNCT BIRD DISTRIBUTIONS ALONG THE WEST SLOPE OF THE PERUVIAN ANDES

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ABSTRACT. Within the steppe-like western slope of the Peruvian Andes forest patches (dry cloud forest) occur from Ecuador to 13°S. Eight sites were studied between Huamba and Zárate. A total of 124 taxa were used to analyze disjunctions. Species numbers decrease from N to S along a gradient of decreasing rainfall. Group 1 taxa (102 species and subspecies) occur from Ecuador south. Nine distributional limits exist. Group 2 taxa (22 species and subspecies) include endemics. Five areas of taxon replacement were identified. The major replacement area is near the Rio Santa Valley. Birds now living in dry cloud forests along the western Andes originated north of this region. Distribution gaps have played an important role in the history of the taxa.

Keywords: Zoogeography, disjunction, Andes, dry cloud forests, Peru.

INTRODUCTION

The Pacific slope of the Peruvian Andes is dominated by arid, steppe-like vegetation types. However, many small forest patches occur in this dry zone between 2400 and 3000 m, forming the richest communities of the western slope of the Peruvian Andes (Koepcke, H.W. 1961, Valencia & Franke 1980, Franke & Valencia 1984). In northern Peru these dry cloud forests occupy extensive and relatively continuous areas, but further south they occur in increasingly smaller and more isolated patches, to about 13°S (Koepcke, H.W. 1961, Valencia 1990). These disjunct forests are thought to represent fragments of a formerly more continuous forest zone (Koepcke, M. 1958; Koepcke, H.W. 1961).

The floristic and faunistic affinities between west slope and east slope forests, as well as the existence of low passes in northern Peru, especially the Porculla Pass (2145 m), led to the hypotheses that east slope species (1) crossed the low passes to the west, and (2) dispersed southward through the forest belt (Koepcke, M. 1958, 1961b, Koepcke, H.W. 1961, Simpson 1975). Biogeographers accept the idea that the Andean montane forests were more continuous when depressed altitudinally during cool, humid glacial periods. At such times temperate and subtropical zones were located along less dissected lower slopes. Conversely, the upward shift of climatic zones during interglacial periods led to increasing fragmentation of montane vegetation (Haffer 1987), thus isolating bird populations and playing a role in speciation along the western Peruvian Andes.

METHODS

Field studies were made at 8 dry cloud forest sites between 2500 and 3000 m, from 4°41'S, near the Ecuadorian border, to 11°55'S in central Peru: (1) Huamba, Department of Piura (4°41'S, 2900 m); (2) Chiñama, Lambayeque (6°06'S, 2550 m); (3) Llaguén, La Libertad (7°42'S, 2600 m); (4) Cochabamba, Ancash (9°27'S, 2800 m);

(5) Wiñapajatun, Ancash (9°41'S, 2600 m); (6) Noqno, Ancash (10°03'S, 2850 m); (7) Linday, Lima (11°50'S, 3000 m), and (8) Zárate, Lima (11°55'S, 2850 m).

Distributional records of the species observed at the 8 sites (Appendix 1) are based on the author's field work, museum specimens (Museo de Historia Natural, Universidad de San Marcos, Lima; Louisiana State University Museum of Natural History, Baton Rouge; National Museum of Natural History, Washington; Field Museum of Natural History, Chicago; and British Museum of Natural History, Tring), and the literature (Koepcke M. 1958, 1961a, b, 1965, Valencia & Franke 1980, Franke & Valencia 1984, Hellmayr, Conover & Cory 1918-1949, Zimmer 1931-1975, Fjeldsa & Krabbe 1990, Parker et al. 1985, Meyer de Schauensee 1966, Schulenberg 1987, Schulenberg & Parker 1981, Parker 1981, O'Neill & Schulenberg 1979, Plenge 1974). For each species the records were plotted on a map of the study area in order to determine the latitudinal limits of each species.

After eliminating low altitude species that reach the dry cloud forests only occasionally, a list of 128 species was obtained. For 9 of these species only scattered records exist and these species were eliminated. In several of the 119 remaining species, more than one subspecies occur in the study area. Given relatively minor differences between most subspecies, geographic variation may actually be clinal. Since subspecies present difficulties in biogeographic analysis (Cracraft 1985) they were avoided, with one exception. Four species have morphologically distinct subspecies ranging along the latitudinal gradient studied: *Cranioleuca antisiensis* (3 subspecies), *Aglaeactis cupripennis* (2), *Lepthastenura pileata* (2) and *Atlapetes seebohmi* (2). In spite of Cracraft's (1985) caveat I have included the subspecies of these four species because they are well marked and present interesting distributional information. Thus, 124 taxa (116 species and 8 subspecies) were analyzed in the present paper.

RESULTS

The number of species in dry cloud forests decreases markedly from north to south, from 102 species in northwestern Peru to 56 in central Peru (Figure 1). The N - S decrease in species numbers is significantly correlated ($r=0.8723$, $P>0.001$) with the gradient of decreasing rainfall. In turn vegetation characteristics of the dry cloud forests reflect the rainfall gradient (Valencia 1990).

The 124 taxa are divided into two groups. In the first group I place 102 taxa that occur in Ecuador and have a continuous or nearly continuous distribution southward to a certain point along the western slope. In the second group (22 taxa) I include species and subspecies that do not occur in Ecuador, but have a continuous or relatively continuous distribution along part of the western slopes (Appendix 1).

DISTRIBUTION PATTERNS OF GROUP 1 TAXA

The 102 taxa in group 1 can be divided into nine subgroups, with southern limits at the following areas: (1) Porculla Pass (7 taxa, 5°51'S); (2) Chiñama (7 taxa, 6°06'S); (3) Rio Chancay Valley (4 taxa, 6°40'S); (4) Rio Saña Valley (26 taxa, 6°54'S); (5) Rio Jequetepeque Valley (2 taxa, 7°19'S); (6) Rio Chicama Valley (4 taxa, 7°29'S);

(7) Llaguén (8 taxa, 7°42'); (8) Cordilleras Blanca and Negra (5 taxa, ca. 10°S); (9) 39 taxa occurring at the southern limit of the study area (11°55'S) but not necessarily having their southern distributional limit there.

A plot of numbers of taxa in group 1 against latitude shows a N - S decreasing trend (Figure 1). This trend is highly correlated with the rainfall gradient ($r = 0.9128$, $P < 0.001$) and very similar to the trends obtained for vegetation parameters (number of woody species, density, basal area and vertical structure; Valencia 1990). These results strongly suggest that climate and habitat conditions are important factors in these distributions patterns.

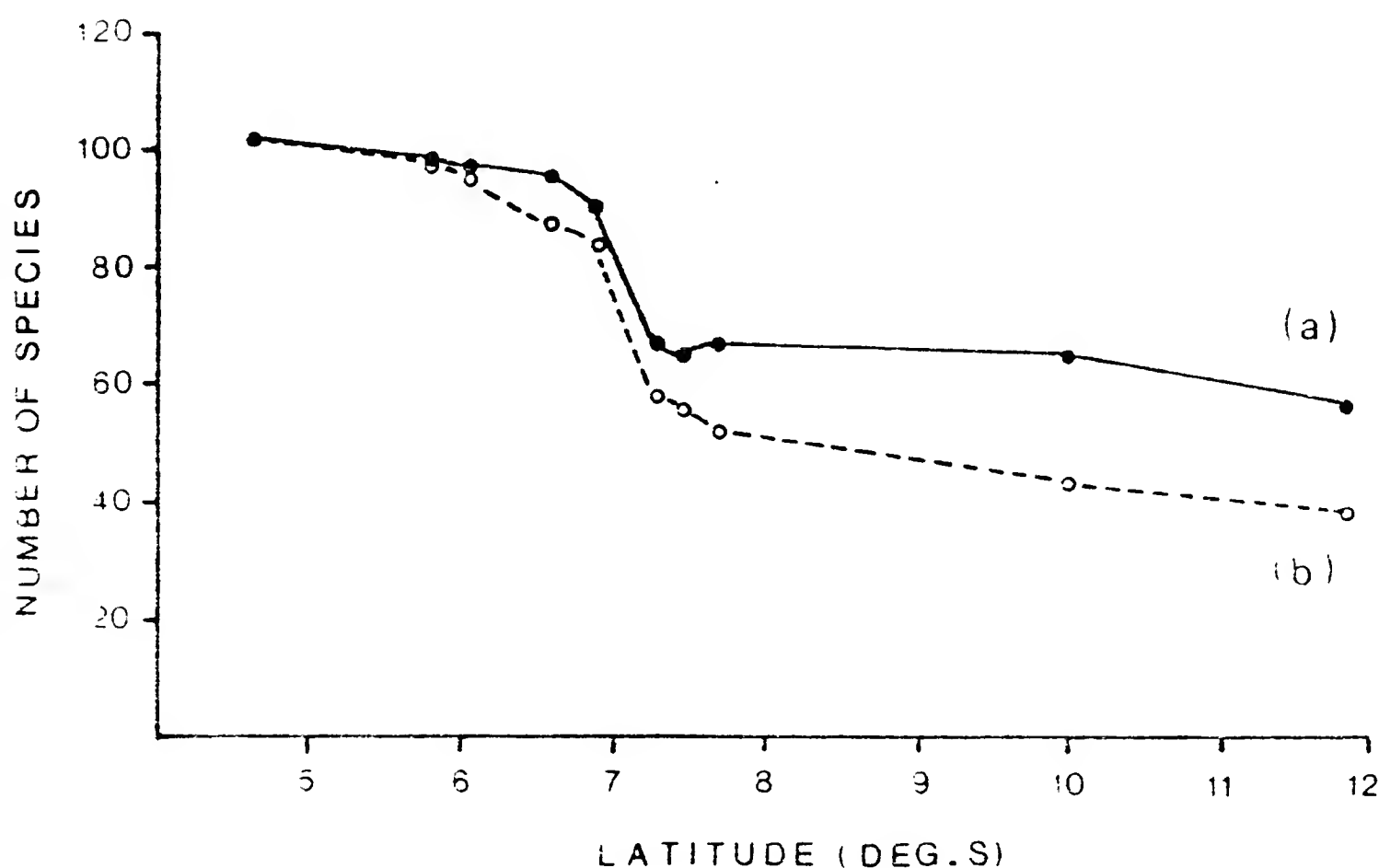


FIGURE 1 - Number of avian taxa occurring in dry cloud forests along the western slope of the Peruvian Andes. a) Total number of taxa b) Taxa with distributions extending from Ecuador southward.

DISTRIBUTION PATTERNS OF GROUP 2 TAXA

The second group consists of 22 taxa including species endemic to western Peru, several of which have a very restricted distribution. Nine subgroups of closely related taxa replace each other latitudinally along the study area (Figure 2). Three of these subgroups consist of subspecies: *Cranioleuca antisiensis* (3 subspecies), *Lepthastenura pileata* (2) and *Aglaeactis cupripennis* (2). Three subgroups consist of species that are often treated as subspecies: *Anairetes nigrocristatus* and *A. reguloides*, *Saltator nigriceps* and *S. aurantirostris*, and *Atlapetes seebohmi* and *A. nationi*. Finally, the last three subgroups consist of congeneric species: *Synallaxis elegantior* and *S. zimмери*, *Ochthoeca piurae* and *O. leucophrys*, and *Diglossa humeralis* and *D. brunneiventris*. Only two of these subgroups show distributional overlap (*Anairetes* and *Ochthoeca* species), where the deep Rio Santa Valley separates the Cordilleras Blanca and Negra.

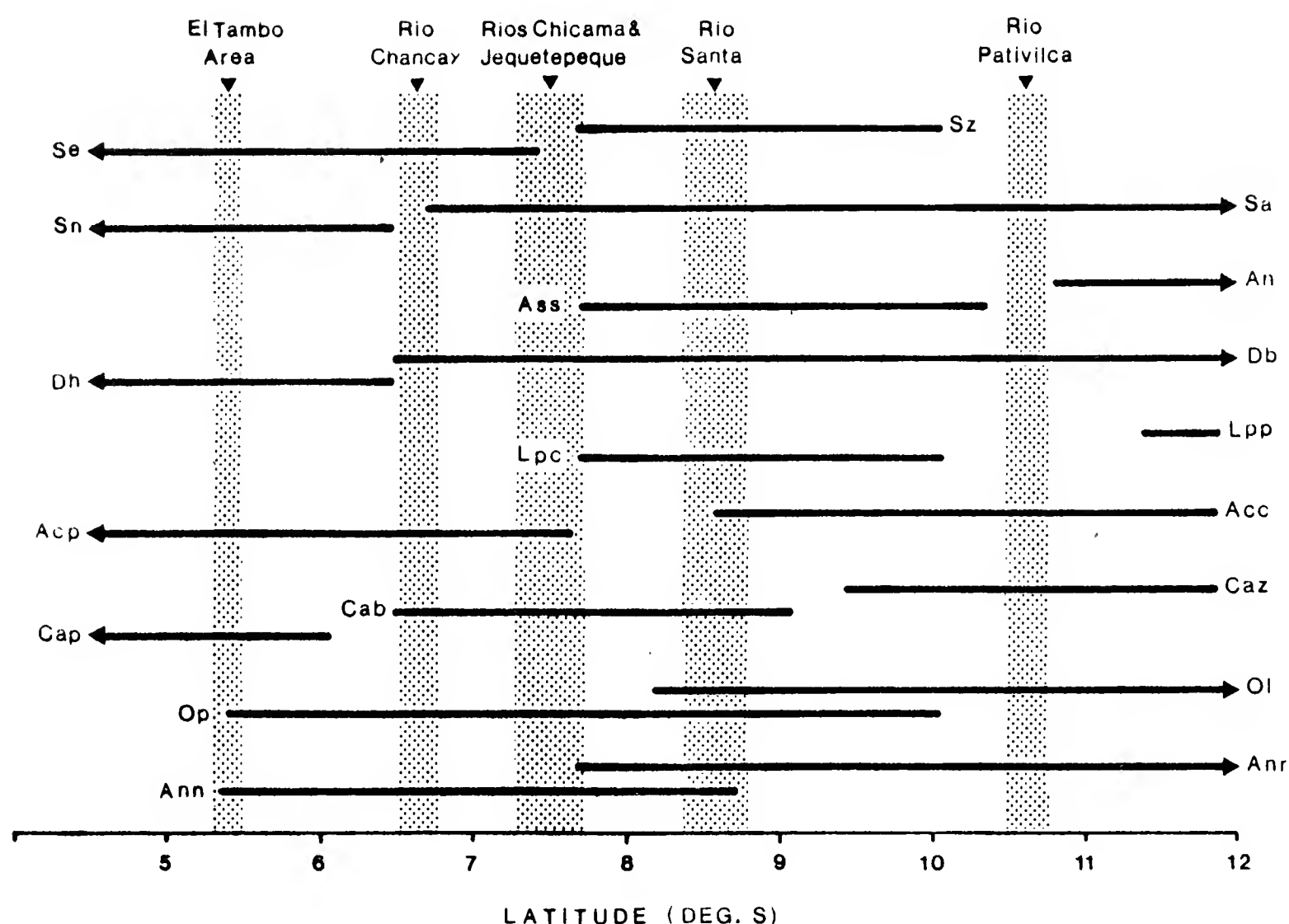


FIGURE 2 - Latitudinal distribution of nine groups of related taxa that replace each other along the western slope of the Peruvian Andes. Abbreviations: Ann, *Anairetes nigrocristatus*; Anr, *A. reguloides*; Op, *Ochthoeca piurae*; Ol, *O. leucophrys*; Cap, *Cranioleuca antisiensis palamblae*; Cab, *C. a. baroni*; Caz, *C. a. zaratensis*; Acp, *Aglaeactis cupripennis parvulus*; Acc, *A. c. caumatonotus*; Lpc, *Lepthastenura pileata cajabambae*; Lpp, *L. p. pileata*; Dh, *Diglossa humeralis*; Db, *D. brunneiventris*; Ass, *Atlapetes seebohmi seebohmi*; An, *Atlapetes nationi*; Sn, *Saltator nigriceps*; Sa, *S. aurantirostris*; Se, *Synallaxis elegantior*; Sz, *S. zimneri*. Shaded areas: major areas of species or subspecies replacement.

Five major areas of species or subspecies replacement or range limits (Figure 2) are listed below.

- (1) Around 5°20'S, near El Tambo, Piura; northern limit of *Anairetes nigrocristatus* and *Ochthoeca piurae*.
- (2) Around 6°30'S, near Llama and Chugur, Cajamarca, deep valley of Rio Chancay (upper Rio Reque); contact between *Diglossa humeralis* and *D. brunneiventris* (Graves 1982, Vuilleumier 1984), replacement of *Saltator nigriceps* by *S. aurantirostris* and *Cranioleuca antisiensis palamblae* by *C.a. baroni*.
- (3) Around 7°30'S, near Huacraruco, Sunchubamba and Llaguén, deep valleys of Rios Jequetepeque and Chicama; replacement of *Synallaxis elegantior* by *S. zimneri*, southern limit of *Aglaeactis cupripennis parvulus*, northern limit on the western slope of *Atlapetes seebohmi seebohmi*, *Lepthastenura pileata cajabambae*, *Anairetes reguloides*, *Polyonymus caroli*, and *Chrysophilus atricollis*.

- (4) Between 8°30' and 9°S, Rio Santa Valley. Area no. 4 is particularly important. The Rio Santa is the largest river of the Pacific watershed and forms the largest valley of western Peru. The upper Rio Santa, running for 180 km parallel to the coast before turning westward separates the eastern and very high Cordillera Blanca from the western, lower Cordillera Negra. Avian distribution patterns in this area are complex.

Most species occurring north of the Rio Santa Valley have a relatively extensive range and are present in both the Cordilleras Blanca and Negra. A few species, however, have only been reported from the Cordillera Blanca (e.g. *Mecocerculus leucophrys*, *Ochthoeca rufipectoralis*). Four of the groups of taxa (see above) show replacement or separation in the Rio Santa Valley. (1) Northerly *Anairetes nigrocristatus* occurs in the Cordillera Blanca, whereas southerly *A. reguloides* occurs in the Cordillera Negra. There is only one possible record of *reguloides* from the Cordillera Blanca (Frimer & Nielsen 1989). (2) *Cranioleuca antisimensis baroni* (northerly), occurs only in the Cordillera Blanca, whereas *C. a. zaratensis* (southerly), occurs in the Cordillera Negra. Fjeldsa and Krabbe (1990:358-359) consider *baroni* a full species. They further state that *C. baroni baroni* "crosses to Pacific slope of Cordillera Negra" in Ancash. However, the 9 specimens collected during my study in the Cordillera Negra (Ancash) have the same characters as the 10 specimens of *zaratensis* from the Department of Lima and not the characters of *baroni*. (3) *Aglaeactis cupripennis caumatonotus* occurs on both cordilleras, but has not been recorded on the western slope north of the Santa Valley, where the specimens available correspond to *A. c. parvulus*. (4) *Ochthoeca piurae* and *O. leucophrys* are sympatric in the Cordillera Negra, but the latter species also occurs in the Cordillera Blanca. It is noteworthy that *Synallaxis zimneri*, like *O. piurae* an endemic species restricted to a small area of the Pacific slope, occurs along the Cordillera Negra and further north in Lambayeque. These taxa have not yet been recorded from Cordillera Blanca or any other locality within the Santa Valley.

- (5) Around 10°30'S, Rio Pativilca Valley; replacement of *Lepthastenura pileata cajabambae* by *L. p. pileata* and *Atlapetes seebohmi seebohmi* by *A. nationi*; southern limit of *Synallaxis zimneri* and *Ochthoeca piurae*.

DISCUSSION

Northern origin

The distribution patterns described in this paper, especially the patterns of species replacement and/or species limits at given areas along the western slope of the Peruvian Andes, supports the concept of a northern origin for most avifaunal elements of dry cloud forests. The N - S decrease in species numbers is also correlated to the decrease in rainfall and associated vegetation parameters (number of woody species, density, basal area and vertical structure, Valencia 1990). Thus, historical as well as ecological factors have had important effects on avian distribution.

The complex distribution patterns found in Ancash also support the idea of a northern origin. If the species dispersed from north to south, they would be expected to have occupied the appropriate habitats in the Rio Santa Valley, including the

Cordillera Blanca, before they dispersed to the Cordillera Negra. Several species with a southern limit in Ancash show this pattern, as do also the *Cranioleuca* and *Anairetes* groups. In these instances, the northern species (or subspecies) occupies the Cordillera Blanca, whereas the southern one occurs from the Cordillera Negra southward.

The distribution of *Synallaxis zimmeri* and *Ochthoeca piurae* does not correspond to this pattern, however. These 2 species occur north of the Santa Valley, in La Libertad and along the Cordillera Negra, but they are not recorded in the Santa Valley. The differences between the patterns in *Cranioleuca* and *Anairetes* on the one hand, and in *S. zimmeri* and *O. piurae* on the other, can be explained by the fact that species occupying the interior of the Santa Valley, Cordillera Blanca, range up to around 4000 m, whereas *Synallaxis zimmeri* and *Ochthoeca piurae* occur lower, from 1500-1800 m to about 2800 m. Both species occur in open, dry habitats as well as in dry cloud forests. It is thus not surprising that these species did not reach the upper Santa Valley, but instead dispersed southward along the lower slopes.

Efficacy of barriers

Although the efficacy of low passes in the western cordillera as barriers to dispersal of montane species has been questioned (Parker et al. 1985), it is intriguing to note that many range limits coincide with areas where the western Andes are lowest (Vuilleumier 1969, 1977) and with the deepest valleys of the Pacific drainage. This distribution gap could be an artifact resulting from incomplete sampling in the area. Only further investigation will resolve this issue unequivocally. However, a study of the distribution of 306 dry cloud forest patches shows that several important latitudinal gaps coincide with the low areas of the western Andes and with the deep valleys of the Pacific slope (Valencia 1990). If montane forests were more continuous in the past during cool and humid glacial periods, when they occupied the lower, more continuous mountain slopes, then the low passes and the deep valleys must have played an important role in fragmenting the forest zone as it shifted upward during interglacial periods. The increasing patchiness of the forest resulted probably not only from the more complex topography of the upper slopes (Haffer 1987), but also from the retreat of forest patches to favorable slopes. Valencia (1990) has shown the tendency of forest patches to be restricted to more humid slopes. The low passes must also have had an effect in dissecting the forest area. As mentioned earlier, dry cloud forests occur generally between 2400 and 3000 m. Summits in the low Andes of northwestern Peru are below 3000 m, thus restricting considerably the potential extension of forest. Vuilleumier (1969, 1977, 1984) presented models of the effects of the Pleistocene depression in northern Peru.

Main gaps

Three gaps are especially important. The first gap, between 6°30' and 6°47'S, corresponds to the Rio Chancay (upper Rio Reque) Valley, Cajamarca, where the western Andes are low and narrow. The contact between *Diglossa humeralis* and *Diglossa brunneiventris* is found here (Graves 1982, Vuilleumier 1984). Koepcke (1961b) and Zimmer (1942) considered the low pass in this area to be the dispersal route by which *Cranioleuca antisimensis baroni* and *Cyclarhis gujanensis* reached the western slope. This area may have been more important for dispersal and speciation of birds than the Porculla Pass. Even though Porculla is the lowest pass in northwestern Peru, it occurs in a relatively linear area of the western Andes, thus presenting no special

problem for dispersal (Vuilleumier 1984 discussed the barrier effect of the Porculla Pass and surrounding areas).

The second gap, between 8°28' and 8°49'S, correponds to the Rio Santa Valley and is wide (about 50 km). This valley separates *Cranioleuca antisiensis baroni* from *C. a. zaratensis*, and *Anairetes nigrocristatus* from *Anairetes reguloides*. In both cases the northern taxon occurs in the Cordillera Blanca, while the southern one is distributed from the Cordillera Negra southward.

The third gap, between 10°30' and 10°45'S, corresponds to the Rio Pativilca Valley. This valley separates two pairs of taxa, *Lepthastenura pileata cajabambae* from *L. p. pileata*, and *Atlapetes seebohmi seebohmi* from *Atlapetes nationi*, and marks the southern limit of west slope endemics, *Ochthoeca piurae* and *Synallaxis zimmeri*.

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APPENDIX 1

Avian taxa recorded at 8 dry cloud forest sites along the western slope of the Peruvian Andes. Code number indicates distribution southward from Ecuador. (1) To Porculla Pass, 5°51'S; (2) To Chiñama, 6°06'S; (3) To Rio Chancay Valley, 6°40'S; (4) To Rio Saña Valley, 6°54'S; (5) To Rio Jequetepeque Valley, 7°19'S; (6) To Rio Chicama Valley, 7°29'S; (7) To Llaguén, 7°42'S; (8) To Cordilleras Blanca and Negra, ca. 10°S; (9) To Zárate, 11°55'S. (10) Avian forms that do not occur in Ecuador; (11) Avian forms with scattered records from western Peru; (12) Low altitude species. Taxa are listed as species (family). * Migrant from North America; all other species are "resident".

Distribution pattern 1:

Pipreola arcuata (Cotingidae), *Myiotheretes fumigatus* (Tyrannidae), *Troglodytes solstitialis* (Troglodytidae), *Saltator cinctus* (Cardinalidae), *Hemispingus verticalis* (Thraupidae), *Trogon personatus* (Trogonidae), *Cyanolyca turcosa* (Corvidae).

Distribution pattern 2:

Geotrygon frenata (Columbidae), *Piculus rivolii* (Picidae), *Cranioleuca antisensis palamblae* (Furnariidae), *Phyllomyias uropygialis* (Tyrannidae), *Elaenia pallatangae* (Tyrannidae), *Pachyramphus albogriseus* (Cotingidae), *Catamblyrhynchus diadema* (Catamblyrhynchidae).

Distribution pattern 3:

Diglossa humeralis (Coerebidae), *Saltator nigriceps* (Cardinalidae), *Colibri thalassinus* (Trochilidae), *Lafresnaya lafresnayi* (Trochilidae).

Distribution pattern 4:

Penelope barbata (Cracidae), *Ciccaba albitarsus* (Strigidae), *Coeligena iris* (Trochilidae), *Ensifera ensifera* (Trochilidae), *Pharomachrus auriceps* (Trogonidae), *Lepidocolaptes affinis* (Dendrocolaptidae), *Margarornis squamiger* (Furnariidae), *Pseudocolaptes biossonneautii* (Furnariidae), *Automolus ruficollis* (Furnariidae), *Grallaria ruficapilla* (Formicariidae), *Phyllomyias nigrocapillus* (Tyrannidae), *Mionectes striaticollis* (Tyrannidae), *Contopus fumigatus* (Tyrannidae), *Turdus serranus* (Turdidae), *Atlapetes leucopterus* (Emberizidae), *Atlapetes torquatus* (Emberizidae), *Tangara viridicollis* (Thraupidae), *Anisognathus lacrymosus* (Thraupidae), *Thraupis cyanocephala* (Thraupidae), *Hemispingus superciliaris* (Thraupidae), *Diglossa cyanea* (Coerebidae), *Myioborus melanocephalus* (Parulidae), *Basileuterus coronatus* (Parulidae), *Conirostrum sitticolor* (Coerebidae), *Cyclarhis gujanensis* (Vireonidae), *Vireo gilvus* (Vireonidae).

Distribution pattern 5:

Accipiter striatus (Accipitridae), *Synallaxis elegantior* (Furnariidae).

Distribution pattern 6:

Mecocerculus stictopterus (Tyrannidae), **Catharus fuscater* (Turdidae), *Atlapetes rufinucha* (Emberizidae), *Tangara vassorii* (Thraupidae).

Distribution pattern 7:

Adelomyia melanogenys (Trochilidae), *Aglaeactis cupripennis parvulus* (Trochilidae), *Heliangelus viola* (Trochilidae), *Scytalopus unicolor* (Rhinocryptidae), *Hemispingus melanotis* (Thraupidae), *Myioborus miniatus* (Parulidae), *Basileuterus nigrocristatus* (Parulidae), *Basileuterus trifasciatus* (Parulidae).

Distribution pattern 8:

Veniliornis fumigatus (Picidae), *Turdus fuscater* (Turdidae), *Nyctidromus albicollis* (Caprimulgidae), *Mecocerculus leucophrys* (Tyrannidae), *Ochthoeca rufipectoralis* (Tyrannidae).

Distribution pattern 9:

Nothoprocta pentlandii (Tinamidae), *Geranoaetus melanoleucus* (Accipitridae), *Buteo polyosoma* (Accipitridae), *Falco sparverius* (Falconidae), *Columba fasciata* (Columbidae), *Zenaida auriculata* (Columbidae), *Leptotila verreauxi* (Columbidae), *Aratinga wagleri* (Psittacidae), *Glaucidium jardinii* (Strigidae), *Caprimulgus longirostris* (Caprimulgidae), *Colibri coruscans* (Trochilidae), *Patagona gigas* (Trochilidae), *Lesbia nuna* (Trochilidae), *Metallura tyrianthina* (Trochilidae), *Ampelion rubrocristatus* (Cotingidae), *Elaenia albiceps* (Tyrannidae), *Anairetes parulus* (Tyrannidae), *Contopus cinereus* (Tyrannidae), *Ochthoeca jelskii* (Tyrannidae), *Myiotheretes striaticollis* (Tyrannidae), *Agriornis montana* (Tyrannidae), *Muscisaxicola maculirostris* (Tyrannidae), *Myiarchus tuberculifer* (Tyrannidae), *Notiochelidon murina* (Hirundinidae), *Notiochelidon cyanoleuca* (Hirundinidae), *Cinclus leucocephalus* (Cinclidae), *Troglodytes aedon* (Troglodytidae), *Turdus chiguanco* (Turdidae), *Zonotrichia capensis* (Emberizidae), *Phrygilus plebejus* (Emberizidae), *Catamenia analis* (Emberizidae), *Catamenia inornata* (Emberizidae), *Pheucticus chrysogaster* (Cardinalidae), *Thraupis bonariensis* (Thraupidae), *Piranga flava* (Thraupidae), *Thlypopsis ornata* (Thraupidae), *Diglossa sittoides* (Coerebidae), *Conirostrum cinereum* (Coerebidae), *Carduelis magellanica* (Carduelidae).

Distribution pattern 10:

Leptasthenura pileata pileata (Furnariidae), *Atlapetes nationi* (Emberizidae), *Leptasthenura pileata cajabambae* (Furnariidae), *Synallaxis zimmeri* (Furnariidae), *Atlapetes seebohmi seebohmi* (Emberizidae), *Ochthoeca piurae* (Tyrannidae), *Aglaeactis cupripennis caumatonotus* (Trochilidae), *Cranioleuca antisiensis zaratensis* (Furnariidae), *Asthenes pudibunda* (Furnariidae), *Ampelion stresemanni* (Cotingidae), *Phrygilus fruticeti* (Emberizidae), *Poospiza rubecula* (Emberizidae), *Cranioleuca antisiensis baroni* (Furnariidae), *Polyonymus caroli* (Trochilidae), *Chrysoptilus atricollis* (Picidae), *Anairetes reguloides* (Tyrannidae), *Aeronautes andecolus* (Apodidae), *Metallura phoebe* (Trochilidae), *Saltator aurantirostris* (Cardinalidae), *Diglossa brunneiventris* (Coerebidae), *Metriopelia ceciliae* (Columbidae), *Ochthoeca leucophrys* (Tyrannidae).

Distribution pattern 11:

Claravis mondetoura (Columbidae), *Bolborhynchus orbygnesi* (Psittacidae), *Otus koepckeae* (Strigidae), *Otus* sp (Strigidae), *Aegolius harrissi* (Strigidae), *Uropsalis segmentata* (Caprimulgidae), **Catharus ustulatus* (Turdidae), *Atlapetes seebohmi simonsi* (Emberizidae), *Pipraeidea melanonota* (Thraupidae).

Distribution pattern 12:

Columbina cruziana (Columbidae), *Amazilia amazilia* (Trochilidae), *Thaumastura cora* (Trochilidae), *Myrtis fanny* (Trochilidae), *Piculus rubiginosus* (Picidae), *Myiopagis subplacens* (Tyrannidae), *Euscarthmus meloryphus* (Tyrannidae), *Pachyramphus homochrous* (Cotingidae), *Campylorhynchus fasciatus* (Troglodytidae), *Turdus reevei* (Turdidae), *Poospiza hispaniolensis* (Emberizidae), *Parula pitiaiyumi* (Parulidae), *Dives warszewiczi* (Icteridae).

SPECIATION IN PATAGONIAN BIRDS

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ABSTRACT. The 138 genera and 218 species of landbirds and waterbirds breeding in Patagonia (south-temperate South America) were surveyed for evidence of speciation phenomena, especially presence of geographical isolates, secondary contact zones, and broad geographic overlaps between closely related congeners. Many of the speciation patterns revealed in this analysis can be correlated with late Pleistocene vicariance events associated with glaciation cycles.

Keywords: South America, Patagonia, biogeography, avifauna, speciation, vicariance, Pleistocene events.

INTRODUCTION

In order to expand the geographic scope of my studies of speciation in Andean birds, I surveyed the 138 genera and 218 species of land- and waterbirds breeding in Patagonia (south-temperate South America from 36°-38°S to about 56°S). In this report I describe speciation phenomena in selected taxa of Patagonian birds, in an attempt to: (a) identify the ecological and geographical circumstances permitting speciation to take place today, and (b) verify the hypothesis that environmental changes in the late Pleistocene were conducive to speciation. The present paper is parallel to an essay on speciation in high Andean birds presented at the XVIIth I.O.C. (Vuilleumier 1980) and is written in the same format to facilitate comparisons.

METHODS AND MATERIAL

Assumptions

As in my survey of high Andean birds I assume that speciation is allopatric (Mayr 1963) and that vicariance events can be reconstructed after "one assesses phylogenetic relationships among species, maps their distribution, and documents the nature of isolation or sympatry among taxa of a given genus" (Vuilleumier 1980: 1256). Four kinds of phenomena are important in this regard (1) geographical isolates within species; (2) geographical isolates between semispecies and allospecies (Amadon 1966); (3) secondary contacts between formerly isolated species-level taxa; and (4) broad range overlaps between closely related congeners (sister species).

Patagonian vegetation and avifauna

Temperate rainforests dominated by beech (*Nothofagus*) in western Patagonia, and dry to arid steppes with tussock grass or scrub east of the Andes, are the two main vegetation types. Other vegetation formations (Magellanic moorland and alpine scrub) cover smaller areas (Hueck & Seibert 1972).

I assign 229 species (11 oceanic, 53 littoral or freshwater, and 165 terrestrial) to the breeding avifauna. The 11 oceanic species (Spheniscidae, Diomedidae,

Procellariidae, Hydrobatidae, Pelecanoididae, Sulidae) are excluded from the survey, which deals with 218 species (53 aquatic, 165 terrestrial).

The analysis is based on a combination of museum and literature research, supplemented by extensive field work (February-March 1965, November-December 1985, February-March 1987, October 1987, January 1988, November 1988).

RESULTS

Geographical isolates within species

INTRA-PATAGONIAN DISJUNCTIONS (1) *Phalacrocorax atriceps* (Phalacrocoracidae). *P. atriceps* and *P. albiventer* are considered conspecific (Devillers & Terschuren 1978; Siegel-Causey 1986). Coastal areas. Isolated populations breed on inland lakes in northern Patagonia (*lacustris*; Navas 1970) and southern Patagonia (Reynolds 1934). These isolates are separated from littoral populations by landscapes including forest, steppe, and mountain.

(2) *Cinclodes oustaleti* (Furnariidae). Alpine vegetation. The northern Patagonian populations (*oustaleti*) are separated from the southern ones in the Tierra del Fuego archipelago (*hornensis*) by a large hiatus (Vuilleumier unpubl.; map in Fjeldså & Krabbe 1990). The nature of the barrier is unclear, since suitable looking habitat occurs in much of the intervening montane region.

(3) *Leptasthenura aegithaloides* (Furnariidae). Open scrub and thorny bushes. An isolated population as discovered and studied by Vuilleumier (unpubl.) in 1985-1988 in NW Tierra del Fuego. The nearest known mainland population (Vuilleumier unpubl.) occurs across the Strait of Magellan in Magallanes.

(4) *Xolmis pyrope* (Tyrannidae). Forest and forest edge, locally matorral (Tierra del Fuego). The Chiloé Island population (*fortis*) is weakly differentiated from the mainland one and separated by a narrow water gap (Vuilleumier 1985).

(5) *Cistothorus platensis* (Troglodytidae). Marsh grassland. The Patagonian populations appear to consist of two disjunct groups (11 and 12 in Traylor 1988) that show weak differentiation. The nature of the apparent gap between these isolates may correspond to the area occupied by the Patagonian icecap.

EXTRA-PATAGONIAN DISJUNCTIONS (1) *Pterocnemia pennata* (Rheidae). Grassy steppe. Patagonian populations (*pennata*) are isolated from high Andean ones living in the dry puna (*tarapacensis* and *garleppi*) by a gap (map in Fjeldså & Krabbe 1990) of about 800 km of montane terrain, some of which would appear suitable for occupation (Vuilleumier unpubl.).

(2) *Strix rufipes* (Strigidae). *Nothofagus* forest. The Patagonian form (*rufipes*) is separated from the chaco form (*chacoensis*) (Short 1975) by dry monte woodland and Patagonian steppe.

(3) *Picoides lignarius* (Picidae). *Nothofagus* forest and edge. Two morphologically indistinguishable isolates, one in Patagonia and the other in Bolivia, are separated by about 1000 km of vegetation including woodland, scrub, and monte, partially occupied

by allospecies *mixtus* (Short 1982). Competitive exclusion could maintain the isolation.

Geographical isolates between semi- or allospecies

INTRA-PATAGONIAN DISJUNCTIONS (1) *Pteroptochos* (Rhinocryptidae). The two *Nothofagus*-inhabiting taxa are separated by the Bío-Bío River, *castaneus* occurring north, and *tarnii* south of this barrier. I consider these taxa as members of a superspecies (Vuilleumier 1985) but others (Fjeldså & Krabbe 1990) keep them conspecific.

(2) *Scytalopus* (Rhinocryptidae). Northern taxon *fuscus* (found in more open situations, *contra* Fjeldså & Krabbe 1990) and southern one *magellanicus* (breeding in dense *Nothofagus* forest, again *contra* Fjeldså & Krabbe 1990) appear to meet at or near the Bío-Bío River. Fjeldså & Krabbe (1990) treat these two forms as species that show considerable sympatry. They are borderline cases. Whether there is sympatry seems open to question in the absence of specimen records.

EXTRA-PATAGONIAN DISJUNCTIONS (1) *Charadrius* (Charadriidae). Patagonian taxon *falklandicus* (coastal pebble beaches but also inland areas) is closely related to high Andean *alticola* of the puna (borderline case: they are either subspecies or allospecies), and to New Zealand taxon *bicinctus*. Bock (1958) considers *falklandicus* and *bicinctus* to form a superspecies. He suggested (Bock 1958:88) that "*falklandicus* and *bicinctus* differentiated from each other in Antarctica, one migrating north to South America and the other to New Zealand".

(2) *Gallinago* (Scolopacidae). Patagonian *stricklandii* (boggy areas of Tierra del Fuego and Cape Horn archipelagoes) and high Andean *jamesoni* (páramos and wet edge of puna) are borderline cases, treated by some authors as subspecies (Fjeldså & Krabbe 1990) and by others as species (Hayman et al. 1986). They show morphological differentiation and are separated by about 2000 km of largely unsuitable montane vegetation (too dry). Similarity in aerial displays between South American species (sometimes placed in genus *Chubbia*) and New Zealand snipe (genus *Coenocorypha*) suggests "common ancestry for these two groups of southern hemisphere snipes" (Miskelly 1990).

(3) *Aphrastura* (Furnariidae). Allospecies *masafuerae* (Juán Fernandez Islands) and *spinicauda* (forested mainland) are isolated by 600 km of water (Vuilleumier 1985).

(4) *Sicalis* (Emberizidae). Patagonian allospecies *lebruni* (grassy steppes and dirt banks) and high Andean *olivascens* (scrub and rocky areas) are separated by about 400 km of montane vegetation partly occupied by congener *S. auriventris*, thus suggesting interspecific competition as a factor in maintaining isolation.

Secondary contacts

PARAPATRY (1) *Thinocorus* (Thinocoridae). Closely related and differentiated species *orbignyianus* (Andean) and *rumicivorus* (steppe) are largely allopatric but share a 2000 km-long contact zone along the Andean foothills where overlap is narrow (Maclean 1969; map in Fjeldså & Krabbe 1990).

(2) *Phrygilus* (Emberizidae). Allospecies *gayi* (steppe) and *patagonicus* (*Nothofagus* forest and edge) appear to share a 1500 km-long contact zone along the Andes at the ecotone between these vegetation types (Vuilleumier unpubl.).

HYBRIDIZATION (1) *Catharacta* (Stercorariidae). Limited hybridization between allospecies *antarcticus* and *chilensis* has been documented by Devillers (1978) in Santa Cruz.

(2) *Phrygilus* (Emberizidae). A zone of interspecific hybridisation between allospecies *gayi* and *patagonicus* is under study in NW Tierra del Fuego (Vuilleumier unpubl.).

MARGINAL OVERLAPS (1) *Podiceps* (Podicipedidae). The restricted range of *gallardoi* (Patagonia) is entirely subsumed in the extensive range of *occipitalis*. Storer (1982) described a hybrid between the two species. The southern peripheral overlap between *gallardoi* and *occipitalis* is matched, in the high Andean puna, by the one between *taczanowskii* and *occipitalis*. Do these patterns represent double invasions?

(2) *Chloephaga* (Anatidae). The small range of southern Patagonian *rubidiceps* is encompassed within the range of its wider ranging sister species *poliocephala*. This could be an instance of double invasion.

(3) *Geositta* (Furnariidae). The range of southern Patagonian *antarctica* is entirely enclosed within that of widespread *cunicularia*. Habitat co-occupancy has been demonstrated in NW Tierra del Fuego (Vuilleumier unpubl.). This could be another case of double invasion.

(4) *Melanodera* (Emberizidae). The range of southern Patagonian *melanodera* (grassy steppe, moorland) is enclosed within the range of widespread *xanthogramma* (Andean, maritime cliffs in Cape Horn area) (Vuilleumier unpubl.). Again, this could be a double invasion.

Broad range overlaps

(1) *Haematopus* (Haematopodidae). Three species overlap extensively along Patagonian coasts (wide ranging *palliatu*s, southern South American *ater*, Patagonian *leucopodus*). Occasional hybridisation has been demonstrated between *ater* and *palliatu*s and between *ater* and *leucopodus* (Jehl 1978).

(2) *Attagis* (Thinocoridae). The broad overlap zone in the Patagonian Andes between sister species *gayi* and *malouinus* (Hayman et al. 1986, Fjeldså & Krabbe 1990) remains to be demonstrated with specimen data.

(3) *Enicognathus* (Psittacidae). There is broad overlap between *ferrugineus* and *leptorhynchus* in forests of northern Patagonia (Vuilleumier 1985).

DISCUSSION

Range discontinuities occur in a number of Non-Passerine, Non-Oscine, and Oscine species living in forest, steppe, alpine scrub, and along the coast of Patagonia. Most intra-Patagonian differentiation is weak, only a couple of instances existing at the superspecies level (*Pteroptochos*, *Scytalopus*). On the other hand, many extra-Patagonian disjunction patterns involve major differentiation. Geographically, extra-Patagonian vicariance patterns include taxa distributed in other parts of the southern hemisphere as well as taxa distributed elsewhere in South America, especially the Andes.

Whereas the numerous instances of disjunction suggest that speciation is currently very active in and around Patagonia, it is often difficult to pinpoint the nature of the barriers between isolates, both within Patagonia and between Patagonia and other regions. An exception may be the Bío-Bío River isolating *Pterotochos castaneus* and *P. tarnii*, or various water gaps in *Leptasthenura*, *Xolmis*, and *Aphrastura*. In most other cases the nature of the gap cannot be specified at present (examples: *Cinclodes oustaleti*, *Cistothorus platensis*). Some of the large gaps between Patagonian and extra-Patagonian taxa (especially Andean ones) are noteworthy (examples: *Pterocnemia*, *Strix*, *Gallinago*, *Sicalis*). The pattern shown by these and other taxa suggests a common causal factor for such huge and similar geographical gaps. That vicariance events led to the observed isolation seems clear. What is not clear is the nature of the events. Two possibilities can be mentioned. One is deteriorating ecological conditions in the gap area, especially an increase in aridity. The second is the presence of congeneric taxa in the hiatus zone: they could prevent contact through interspecific competition (examples: *Picoides*, *Sicalis*).

Few secondary contacts have been studied in detail in Patagonian birds. Exceptions are *Catharacta* (Devillers 1978) and *Phrygilus* (Vuilleumier unpubl.). Other instances of narrow range overlaps remain elusive, and little concrete evidence actually documents the nature of sympatry (and in *Attagis*, even its existence). Preliminary study of both marginal and broad range overlaps suggests that, as in some of the high Andean cases studied earlier, "closely related species pairs may have only minor habitat differences in sympatry" (Vuilleumier 1980: 1260). An example is the ecological coexistence of *Geositta cunicularia* and *G. antarctica* in NW Tierra del Fuego. In other genera, however, ecological segregation is observed in the zone of sympatry (*Chloephaga*, *Haematopus*, *Melanodera*).

Several appealing models of vicariance involving late Pleistocene glaciation events have been proposed (*Phalacrocorax*, Devillers & Terschuren 1978; *Tachyeres*, Livezey 1986; *Catharacta*, Devillers 1978). These reconstructions dealt with littoral taxa and could be applied to other ecologically similar groups (*Haematopus*). But surely different models must be sought for wholly terrestrial birds. In the past few years I have investigated several landbird genera in detail (*Phalcoboenus*, *Attagis*, *Geositta*, *Cinclodes*, *Phrygilus*). For two of them (*Geositta*, *Phrygilus*) I now have enough data (distributional records, specimens) for attempts at reconstruction of their past histories. These will be presented elsewhere.

The repeated pattern involving two sister species, with one wide-ranging taxon and another with a restricted range in southern Patagonia, found in taxonomically and ecologically diverse genera (*Chloephaga*, *Geositta*, *Melanodera*), suggests double invasion as a common mode of speciation in Patagonia. It is tempting to speculate about the differentiation of small populations in peripherally isolated refuges south of the main icecap at times of glacial maxima, and about a subsequent phase of secondary contact with sympatry, following deglaciation and recolonization by vegetation and consumers (Humphrey & Péfaur 1979).

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GENETIC DIFFERENTIATION IN YELLOWTHROATS (PARULINAE: *GEOTHYLPIS*)

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ABSTRACT. Allozyme variation is analyzed within and among populations of Neotropical and Nearctic species of Yellowthroats (Parulinae: *Geothlypis*). Results indicate that the populations assayed have levels of variability comparable with those of other birds. As indicated by F_{ST} values, heterogeneity tests, and genetic distances among populations, species in the north (*G. trichas*) are less differentiated genetically than Neotropical taxa. The Baja California populations of *G. beldingi* are somewhat differentiated; more so are the Middle American populations of *G. poliocephala*. Differentiation among the Neotropical populations of the *G. aequinoctialis* complex is substantial and coincides with populations having disjunct ranges. It is likely that there is more than one species in this taxon. These results, along with previous findings on Amazonian forest species, indicate that Neotropical avifaunas are more genetically differentiated than are their Nearctic relatives, and suggests that they could be older evolutionarily.

Keywords: *Geothlypis*, parulid warblers, Neotropics, genetic structure, speciation.

INTRODUCTION

As part of a study on the phylogeny of Yellowthroats (Parulinae: *Geothlypis*), I used allozyme electrophoresis to survey genetic variation in a series of populations of nine taxa. This technique provides data for phylogenetic analyses among closely related species, and for estimating parameters of population differentiation within species. Studies of the genetic structure of natural populations provides information critical to an understanding of population dynamics, modes of speciation, and phenotypic diversity (Templeton 1980, Barrowclough 1983, Zink & Remsen 1986).

The study of genetic diversity within and among Neotropical species of birds is in its infancy. In the few species examined to date, workers have found that populations of avian species in Amazonian forests are more structured spatially than are populations of temperate species, but have equivalent levels of genetic variability (Braun & Parker 1985, Capparella & Lanyon 1985, Capparella 1987, Gerwin & Zink 1989, Hackett & Rosenberg 1990, Gill & Gerwin 1989). To place these findings in a broader context, it is critical to investigate species associated with Neotropical habitats other than lowland rainforests. Because of their wide distribution in open wetlands, warblers of the genus *Geothlypis* offer an opportunity to compare genetic variability, population structure, and habitat restriction in both temperate and tropical America.

In this paper, I summarize data obtained from an electrophoresis analysis of members of this complex. My objective is to evaluate the nature of allozymic variation at the population and geographic levels in Neotropical and Nearctic Yellowthroats in the light of our knowledge of other species.

THE YELLOWTHROAT COMPLEX

As currently recognized (American Ornithologists' Union 1983), *Geothlypis* is composed of nine species, most of which are allopatric. *Geothlypis* taxa inhabit marshes, but most forms have broader habitat tolerances, and also occupy other wetlands where tall grass, brush, second growth and sugarcane grow.

In North America, *G. trichas* (Common Yellowthroat) is widely distributed (Figure 1) with populations ranging from completely migratory in the north, to sedentary in central Mexico. In this latter area they co-occur in marshes of the interior valleys with *G. speciosa* (Black-poll'd Yellowthroat). In the southernmost part of its range (South Central Mexico), *G. trichas* also overlaps with *G. poliocephala* (Gray-crowned Yellowthroat); they both breed in sugarcane fields that have replaced natural marshes. None of these instances of sympatry seem to involve close relatives, based on an analysis of plumage characters (Escalante-Pliego, in prep.).

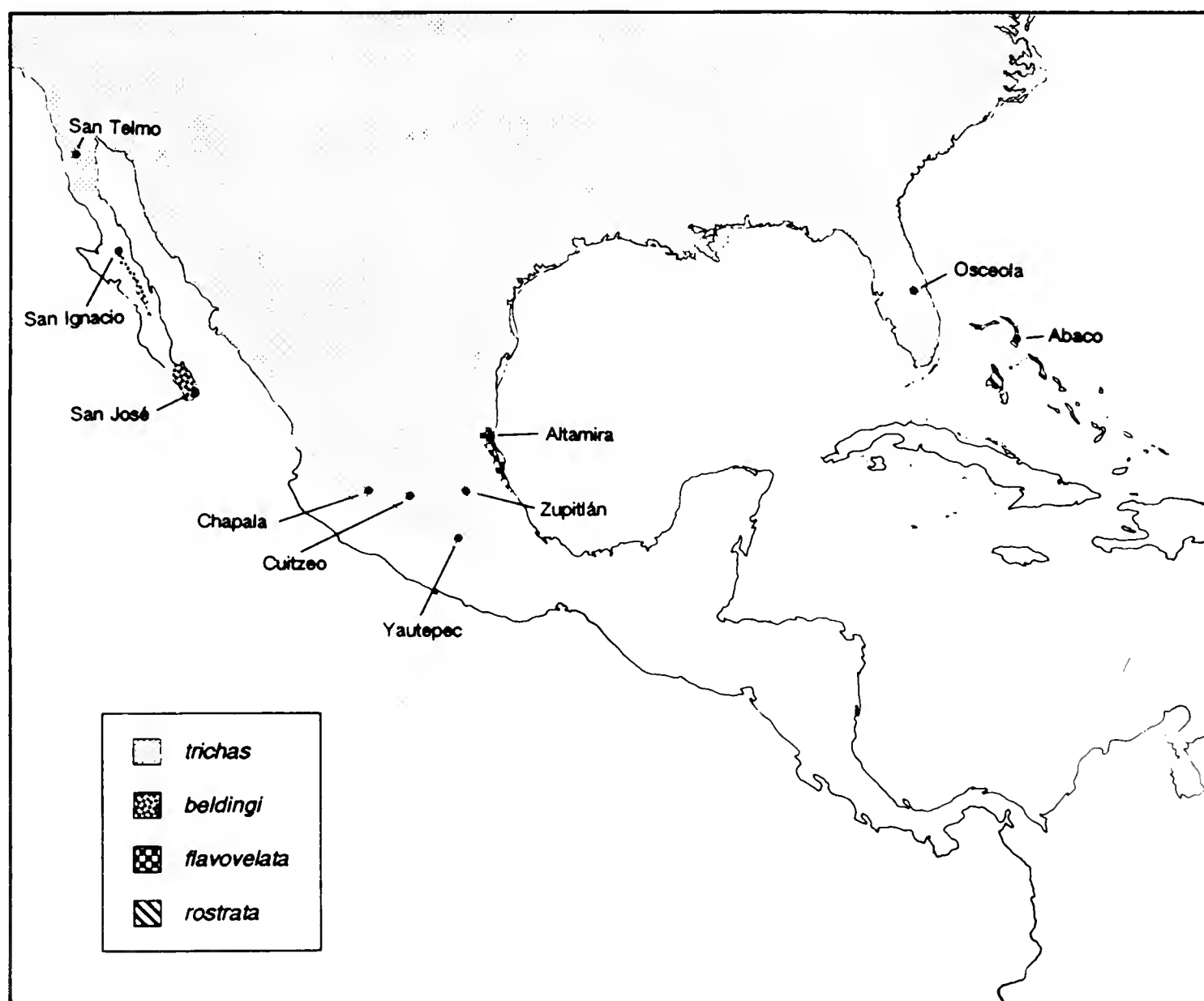


FIGURE 1 – Distributional range of four *Geothlypis* species and sample localities mentioned in the text. US: *Rhode Island* (not in map); Florida, *Osceola*. Bahamas, *Abaco*. México: Hidalgo, *Zupitlán*; Morelos, *Yautepéc*; Michoacán, *Lago de Cuitzeo*; Jalisco, *Lago de Chapala East*; Baja California Norte, *San Telmo*; Baja California Sur, *San Ignacio*; Baja California Sur, *San José*; Tamaulipas, *Altamira*.

Besides *G. speciosa*, forms with restricted ranges also associated with marshes are *G. beldingi* (Belding's Yellowthroat) in the Peninsula of Baja California, and *G. flavovelata* (Altamira Yellowthroat) in northeastern Mexico. Although sharing an affinity for wet habitats, other Yellowthroats have broader habitat tolerances. *G. nelsoni* (Hooded Yellowthroat) is found in Mexico along the humid slopes of the eastern mountains. *G. rostrata* (Bahama Yellowthroat) occurs in bush and abandoned sugarcane fields in some of the Bahama Islands. In the lowlands of Mexico, Central America, and western South America south to Ecuador, *G. poliocephala* and *G. semiflava* (Olive-crowned Yellowthroat) replace each other from north to south near streams in marshy and humid brushy areas of second growth lowland forests. In Nicaragua, Costa Rica, and western Panama, where their ranges are in contact, *G. poliocephala* is found in drier areas (Figure 2).

The South American representative of the group, *G. aequinoctialis* (Masked Yellowthroat) is widely distributed, and occurs in several kinds of wetlands, including marshes. The geographic range of the *aequinoctialis* complex is made up of four disjunct areas (Figure 3): the peripheral form of western Costa Rica and western Panama (*chiriquensis*), sometimes regarded as a separate species (AOU, 1983); the trans-Andean or Pacific slope form (*auricularis* group); and two cis-Andean forms, one north (nominate *aequinoctialis* group), and one south of the Amazon Basin (*velata* group).

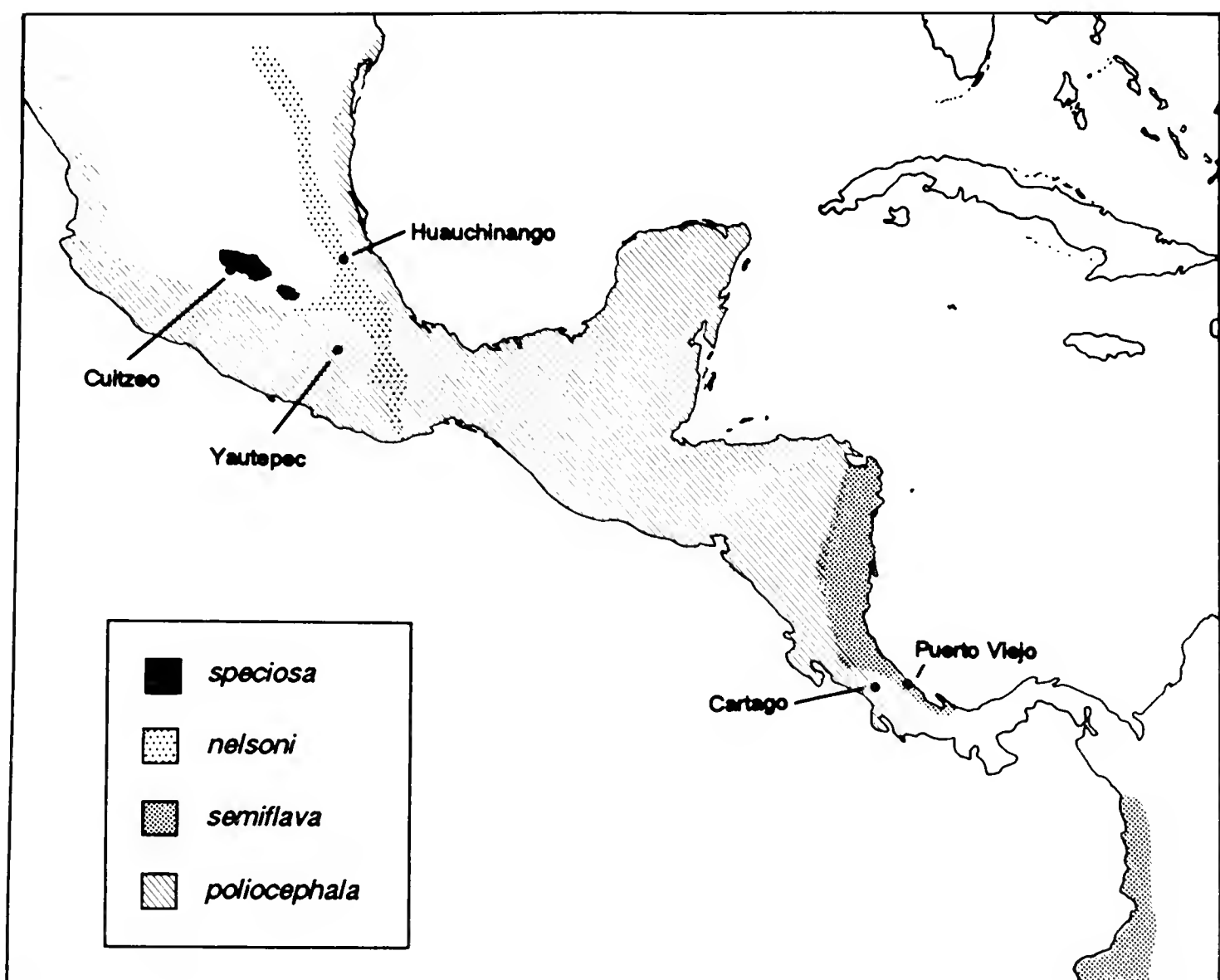


FIGURE 2 – Distributional range of four *Geothlypis* species and sample localities mentioned in the text. Mexico: Michoacan, Lago de Cuitzeo; Morelos, Yautepac; Puebla, Huauchinango. Costa Rica, Cartago; El Limon, Puerto Viejo.

METHODS

Study areas and samples

Samples were collected on breeding grounds in Mexico, Costa Rica, Venezuela, Florida (USA), and the Bahamas, between 1987 and 1989 (Figures 1, 2, and 3). Exact localities are available from the author. The habitat visited in Chapala, Cuitzeo, and Zupitlán is marshland. The marshes of the interior basins of Mexico have been much reduced in the last 500 years through alluviation, desiccation and artificial draining (Tamayo and West, 1964). Aside from marshes, *G. trichas* was found in sugarcane fields around Cuitzeo, and Yautepec. In the arid peninsula of Baja California, marshes are widely scattered. In northern Baja California, *G. trichas* was found along the streams that originate in the western slope of the Sierra de Juárez (San Telmo). In the central desert of the peninsula *G. beldingi* was found in the springs of San Ignacio, and at the southern tip of the Peninsula (San Jose). The extensive marsh at Altamira (Laguna Champayan) receives a large discharge from the Panuco River.

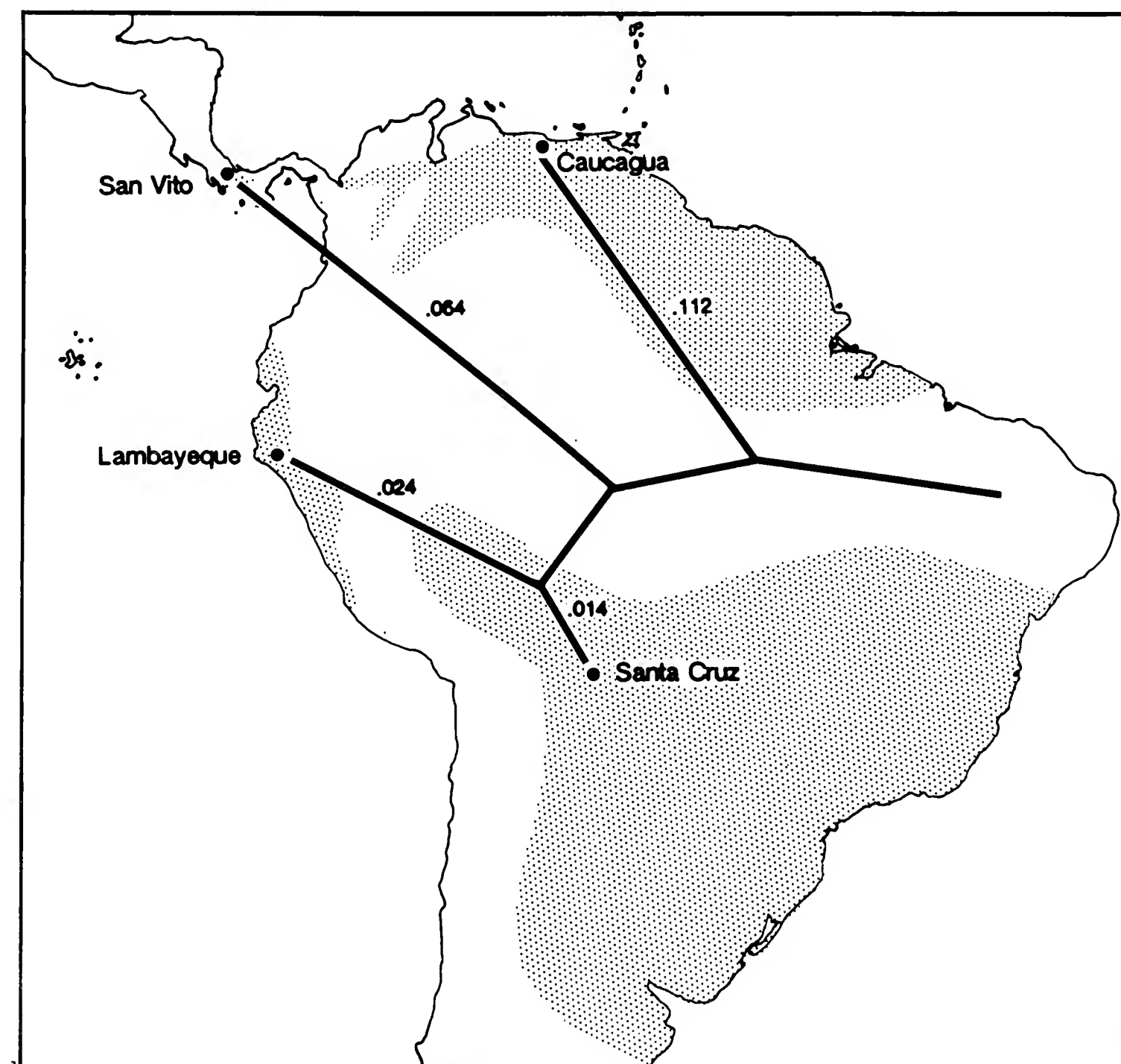


FIGURE 3 – Branching diagram from distance Wagner procedure using Rogers' distances for the four samples of *G. aequinoctialis* superimposed in distributional ranges (Ridgely & Tudor 1989). The lines are not drawn to scale. Localities: Costa Rica, Puntarenas, *San Vito*. Venezuela, Miranda, *Caucaqua*. Peru, *Lambayeque*, Las Pampas. Bolivia, *Santa Cruz*, Velasco.

The lake and inundated area around it extends several hundred square kilometers. At San Vito (Costa Rica) and Caucagua (Venezuela), the habitats where *Geothlypis* was found, are flooded seasonally but are not true marshes; grassy meadows in San Vito, brush and sugarcane fields in Caucagua. The remainder of the localities have a range of open and humid lands or scrub along streams.

Following collection, liver, heart, and breast muscle were preserved in liquid nitrogen until transported to the laboratory, where they were stored at -70°C .

Additional samples from the USA (Rhode Island), Peru, and Bolivia were obtained from other frozen tissue collections (see Acknowledgements).

Electrophoresis

Allozyme variation was assayed for 271 Yellowthroat tissue samples for 32 enzymatic loci following standard techniques (Selander et al. 1971, Harris & Hopkinson 1976, Richardson et al. 1986). The 32 loci scored are: ACON-1, ACON-2, ADA, ADH, DIA, EAP, EST-1, ESTD, FUM, GDA, GDH, GOT-1, GOT-2, GPDH, G-3-PDH, G-6-PDH, IDH-1, IDH-2, LAP, LDH-1, LDH-2, MDH-1, MDH-2, ME, NP, PEP-A, PEP-B, PEP-C, PGM-1, PGM-2, PGM-3, and SDH.

Parameters of genetic variability and differentiation were estimated using several computer programs: BIOSYS-1 (Swofford and Selander 1989) for allelic frequencies, heterozygosities, percent of polymorphic loci, chi square tests of heterogeneity, HardyWeinberg equilibrium tests, Nei's (1978) and Rogers' (1972) genetic distances; NEI2 for heterozygosities and genetic distances, and BOOTFST which provides Wright (1978) F_{ST} values with their confidence intervals calculated through a bootstrap approach.

RESULTS

Genetic Variability.

Of the 32 loci scored, 10 were monomorphic for all populations, 6 were private polymorphisms unique to individual populations, and the other 16 showed shared polymorphisms among populations and/or species. For samples with over five individuals, none of the variable loci showed significant ($P < .001$) departures from Hardy-Weinberg equilibrium. Detailed allelic frequencies will be reported elsewhere (Escalante-Pliego, in prep.). Table 1 shows the average heterozygosity per locus, and the percent of polymorphic loci for each population. Measures of interpopulational differentiation were calculated for species with more than one representative sample.

Population Differentiation in Yellowthroat species.

The samples of the *G. trichas* used in this study comprise a considerable part of the total geographic range. Tests of heterogeneity were not significant for 15 of 19 variable loci. Two loci at which electrophoresis detected substantial geographic differentiation were PGM-1 and PEP-B. At the PGM-1 locus ($P < .001$), the western samples, including San Telmo and three localities of west-central Mexico, shared a polymorphism which was absent in the eastern samples (Rhode Island, Florida, and Zupitlán). At the PEP-B locus the heterogeneity test among populations was significant ($P < .009$); all the samples have the same common allele in frequencies ranging

from 0.5 to 1.0; the frequencies of the less common allele showed no apparent geographic trend. At the G-6-PDH locus, allelic frequencies were significantly different ($P<.045$) because of the absence of an uncommon allele in two populations (Zupitlán and Rhode Island). At SDH a significant difference ($P<.015$) was due to the presence of an allele in the northeasternmost population assayed (Rhode Island). This allele is shared with Bahamian *G. rostrata*. The mean F_{ST} values in the *trichas* complex was 0.077 (95% confidence interval: 0.012-0.112). Averaged Nei's genetic distance for all *G. trichas* populations was 0.004.

TABLE 1 – Genetic variation in populations of *Geothlypis* species calculated over 32 loci.

	Habitat	N	Het	SE	P.L.
<i>Geothlypis trichas</i>					
Rhode Island (USA)	s	13	.0411	(.0160)	22
Osceola (Florida, USA)	s	13	.0449	(.0146)	31
Zupitlán (México)	m	15	.0298	(.0206)	13
Yautepec (México)	c	15	.0322	(.0156)	19
Cuitzeo (México)	m,c	14	.0585	(.0213)	28
Chapala (México)	m	12	.0531	(.0242)	19
San Telmo (México)	s	15	.0509	(.0226)	19
<i>Geothlypis beldingi</i>					
San Ignacio (México)	m	18	.0384	(.0194)	9
San Jose (México)	m	36	.0442	(.0248)	13
<i>Geothlypis flavovelata</i>					
Altamira (México)	m	7	.0633	(.0307)	16
<i>Geothlypis nelsoni</i>					
Huachinango (México)	s	14	.0500	(.0233)	19
<i>Geothlypis rostrata</i>					
Abaco (Bahamas)	s	17	.0481	(.0211)	19
<i>Geothlypis speciosa</i>					
Cuitzeo (México)	m	23	.0106	(.0080)	9
<i>Geothlypis semiflava</i>					
Puerto Viejo (Costa Rica)	s	19	.0343	(.0155)	28
<i>Geothlypis aequinoctialis</i>					
San Vito (Costa Rica)	m	9	.0577	(.0285)	13
Santa Cruz (Bolivia)	m?	2	.0469	(.0345)	6
Lambayeque (Perú)	m?	3	.0521	(.0309)	9
Caucagua (Venezuela)	s	8	.0656	(.0242)	25
<i>Geothlypis poliocephala</i>					
Cartago (Costa Rica)	s	5	.0250	(.0196)	6
Yautepec (México)	c	13	.0478	(.0212)	22

Habitat: s=shrubby and along streams; m = marsh; c = cane fields. N = sample size. Het = Average heterozygosity per locus. P.L. = per cent of polymorphic loci (99% of frequency criterion).

Only the GDA locus showed a significant difference ($P<.005$) between the two samples of *G. beldingi* on the Peninsula of Baja California. The F_{ST} value was 0.059 (95% confidence interval 0.001-0.171); Nei's (1978) genetic distance was 0.011.

The two single samples of *G. poliocephala* came from widely separated areas of their distribution that represent some of the well differentiated subspecies. Tests of heterogeneity were significant for two loci: PEP-C ($P<.001$), and PGM-2 ($P<.07$); the F_{ST}

value was 0.199 (95% confidence interval 0.027-0.281), and Nei's (1978) genetic distance was 0.011.

In *G. aequinoctialis* of South America and Costa Rica, fixed differences were found between various populations at the GDA and ME loci. Differences were also large at other variable loci, giving significant tests of heterogeneity at 8 of 12 loci ($P < .005$ for five loci, $P < .02$ in three loci). This consistent differentiation across loci is reflected in a high F_{ST} value of 0.553 (95% confidence interval: 0.312-0.751). Averaged Nei (1978) genetic distances among the four populations were 0.1245, but the sample from Venezuela had a higher average value (0.1445). The use of Rogers' distances provided similar results. A clustering of Rogers' distances superimposed in the distribution of the *G. aequinoctialis* complex is shown in Figure 3.

DISCUSSION

Levels of intrapopulation variability (Table 1) in *Geothlypis* species are within the range of those previously reported for birds (Braun & Parker 1985, Capparella 1987, Nevo et al. 1984). Due to differences in sample size, and because heterozygosities have large standard errors, a statistical test cannot be performed among the populations associated with different habitats. However, it is noticeable that *G. speciosa* had low heterozygosity and few polymorphic loci. Some populations that are restricted to marshes, such as *G. beldingi* and *G. trichas* of Zupitlán, also have low numbers of polymorphic loci, but similar heterozygosity scores. A dissimilar pattern in other marsh inhabitants is observed in Table 1.

The sample of *G. trichas* from Zupitlán shows some signs of isolation: Zupitlán's average genetic distance of 0.0052 is higher than that of the combined average of all the populations in the *trichas* complex (0.0036). These values are due to significant differences in frequencies at the PGM-1 and PEP-B loci, as mentioned earlier. Zink and Klicka (1990) examined allozyme variation in the *trichas* complex using samples from presumed sedentary (Texas), and migratory (Minnesota) populations, and found an F_{ST} value of 0.04. An equivalent comparison using San Telmo, Rhode Island and Florida samples also yields an F_{ST} value of also 0.04. Considering the sedentary populations in the south only, the F_{ST} value increases to 0.08, but if we ignore Zupitlán, the three remaining populations yield a value of 0.034, similar to the northern part of the *trichas* complex. Because they colonize and breed in sugarcane fields, populations in the rest of the Mexican Plateau perhaps have maintained a larger amount of gene flow in contrast to those of the more arid part of the Plateau where Zupitlán is located.

For other forms, such as *G. beldingi* of Baja California, the scattered distribution of marshes seems to have affected population structure and restricted gene flow. The slight phenotypic differentiation between the two populations is concordant with the slight genetic differentiation in these two populations.

The estimates of F_{ST} and Nei's (1978) genetic distance for the Middle American *G. poliocephala* were approximately twice those in the *trichas* complex and in *beldingi*. This genetic divergence is paralleled by phenotypic distinctiveness.

The results for the *aequinoctialis* complex were more surprising as they suggest more advanced differentiation than the current classification reflects. Very high F_{ST} values, significant tests of heterogeneity, and large genetic distances show a pattern of divergence between the northern Amazonian form *aequinoctialis* and the other three forms. This pattern contrasts with the phenotypic differentiation observed. Plumage patterns are conservative in the complex, except for a reduction of the mask patch in the Pacific slope form (*auricularis*).

In this first study of a non-forest group, the Neotropical species of *Geothlypis* showed increasing levels of population differentiation from north to south. F_{ST} values of Nearctic populations of the *trichas* complex compare well with other values found in warblers of North America, such as 0.03 in well marked subspecies of *Dendroica coronata* (Barrowclough 1980). F_{ST} values increased in the Middle and South American *Geothlypis* species. The genetic distance values obtained here correlate well with values obtained for Parulids (Barrowclough & Corbin 1978), with an average Nei's (1978) genetic distance of 0.100 for species level differentiation. In this context, the four allopatric forms of the *aequinoctialis* complex would seem to deserve species rank.

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BIOGEOGRAPHIC PATTERNS IN BIRDS OF HIGH ANDEAN RELICT WOODLANDS

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ABSTRACT. Woodlands, especially *Polylepis*, form patches in steppe-like Andean habitats at 3500-4500 m. High-elevation woodland is marginal habitat for a number of lower-elevation birds, but there is no direct evidence that colonization at the edge of the ecological range leads to specialization to the new habitat. This happens only after an initial period of entrapment, located away from the founding area, usually on the upper Pacific slope of the Peruvian Andes. Many specialists had east-slope humid forest origins. Other source areas were the eastern premontane woodlands of Bolivia and Argentina, as "entrapment" in the Cochabamba basin was followed by dispersal across Peru. Several levels of differentiation of populations suggest cycles of dispersal and vicariance, but only in a few genera were there speciation events after the initial adaptation to *Polylepis*.

Keywords: Biogeography, Andes, vicariance, refuge theory, *Polylepis* woodlands.

INTRODUCTION

Primary woodlands, especially with *Polylepis*, or with *Gynoxys*, *Buddleia* and various scrubs, form small patches well above the Andean treeline. This habitat may always have been rather localized, but thousands of years of human activity have reduced it to vestiges (Figure 1; Ansión 1986). Most bird species specialized for this habitat thus have relict distributions, and some are extremely rare (Collar et al. MS). This paper discusses biogeographic patterns of these birds.

MATERIALS

High-elevation woodlands in Peru and Bolivia were charted since 1987 (Fjeldså 1987, in press, Fjeldså & Krabbe 1990: 846-7, Frimer & Møller 1989), and this was supplemented with literature surveys and data from museum specimens. Current views on the species' distributions and systematic relationships are in Fjeldså & Krabbe (1990). Relationships, needed to correlate distributions of sister taxa, were evaluated from assumed shared derived character states. In a few cases phylogenetic hypotheses were developed for larger species groups.

THE BIRDS OF *POLYLEPIS* WOODS

Table 1 lists over 100 species living in *Polylepis* woodland. This includes species in adjacent habitats that invade *Polylepis* woodlands locally. Additional hummingbirds, spinetails and tanagers of the humid montane forest visit *Polylepis* seasonally, especially in the northern Andes. Furthermore, a number of birds of prey and some páramo and puna birds use the more open, bushy parts of the woodlands, or roost there. There is continuous variation from these marginal species to those having their

adaptive peaks in high-elevation woodlands (in the following marked with *, or ** for the most specialized). Most specialists are attached to an elevational zone rather than to specific trees, but a few are adapted for searching insects in the multi-layer structure of *Polylepis* bark (*Oreomanes fraseri***, *Leptasthenura xenothorax***; two *Cranioleuca* species*), searching its small-leaved canopy (*Anairetes alpinus***), eating *Polylepis* seeds (*Carduelis crassirostris***) or eating sugary secretions and aphids from associated *Gynoxys* bushes (*Chalcostigma stanleyi**, *Xenodacnis parina**, *Poospiza alticola***). Most specialists are suited for biogeographic studies because of their sedentary habits. They seem able to remain in their tiny "habitat islands" even when snowstorms sweep the highlands (Fjeldså in press b), in contrast to the widespread birds of open highland habitat.

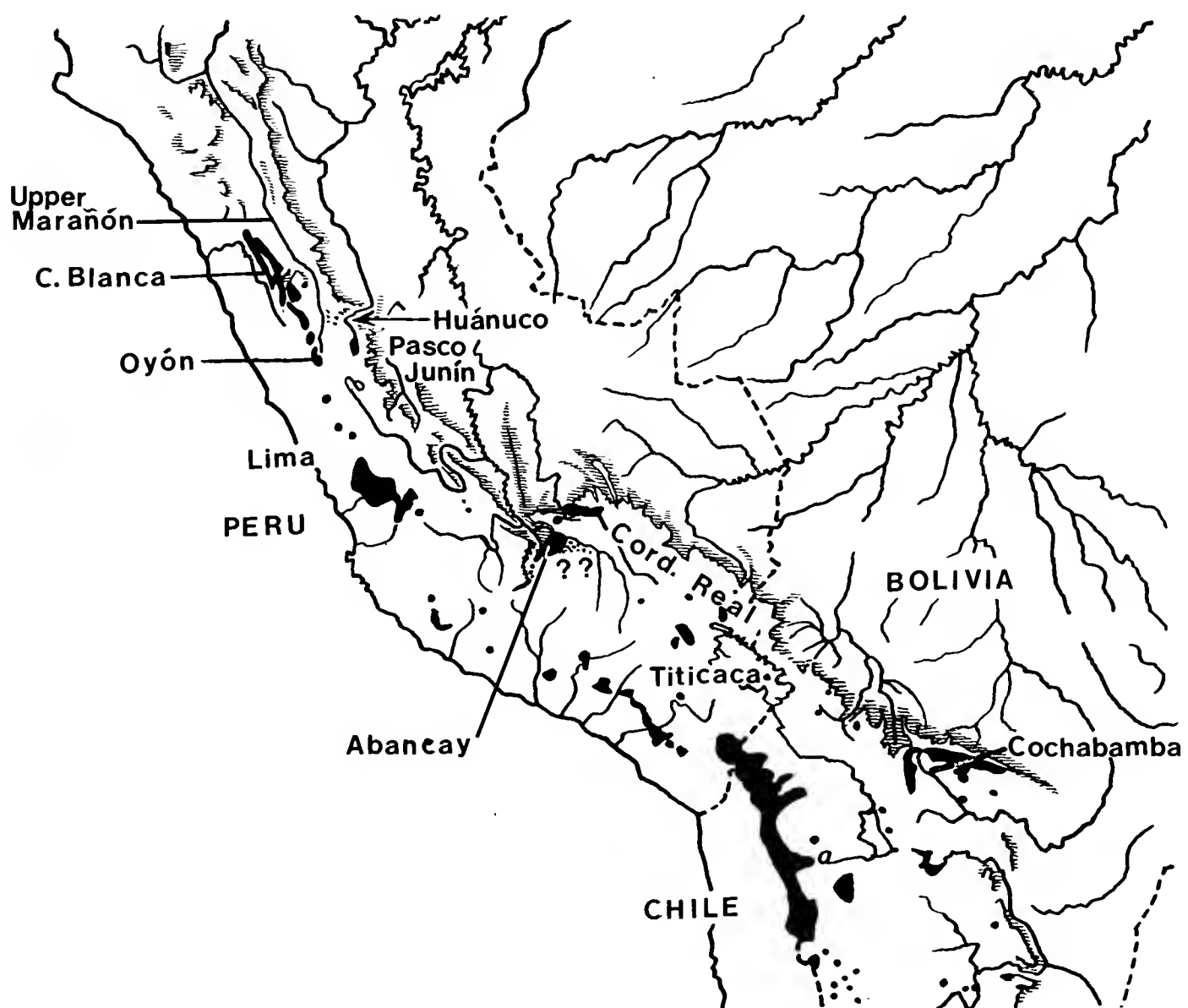


FIGURE 1- High-elevation woodlands in Peru and Bolivia. Black areas have patches of *Polylepis*, mainly at 3500-4500 m elevation. Outside these areas are found few *Polylepis* patches more than a few hectares in area. The shaded zone on the eastern Andean scarps shows treeline at c. 3500 m, sometimes with *Polylepis* admixed. Based on field studies, maps, LANDSAT imagery, and ground surveys.

Faunal provinces

Figure 2 gives examples of patchy, disjunct (relict), and endemic distributions of *Polylepis* birds. Such maps were used to produce summary maps of densities of species richness (Figure 3). The highest species richness is found along the edges of the highlands and in cordilleras intersected by deep valleys. In Peru and Bolivia, many specialists also inhabit altiplanos far from lower-elevation habitat (Figure 3), in contrast to *Polylepis* woodlands north of the North Peru Low (Ecuador), which serve as

TABLE 1 – Species living in *Polylepis* wood at least in part of their range. Legend: High elevation H, * and ** being specialists of woods in this zone. Species with their main distribution on lower elevation or in open habitat are marked ++ if also well established in *Polylepis*, and + if so locally. Habitats: O= open land, U= ubiquitous, S= scrub, Pa= páramo, W= wood, HF= humid forest. Brackets mark assumed sister taxa.

Species	Habitat	Range		
<i>Nothoprocta taczan.</i>	+W	Apurímac	<i>Anairetes alpinus</i>	** C.Blanca C.Real
<i>N. ornata</i>	+OH	Peru-NW Arg.	<i>A. nigrocristatus</i>	++S C.Blanca
<i>Columba maculosa</i>	+W	Peru-Bol.	<i>A. reguloides</i>	+S SW Peru
<i>Bolborhynchos aymara</i>	++S	Bol-W Arg.	<i>A. parulus</i>	++S S Col-S Chile
<i>B. aurifrons</i>	+OH	Peru-NW Arg.	<i>Ochthoeca rufipect.</i>	+W-HF Col-Bol.
<i>B. orbygniesius</i>	++W	Peru-Bol.	<i>O. fumicolor</i>	+Pa-HF Ven-Bol.
<i>Caprimulg. longirost.</i>	++U	Andean	<i>O. oenanthoides</i>	*(OH) Peru-Bol.
<i>Colibri coruscans</i>	+W	Ven-NW Arg.	<i>O. leucophrys</i>	+S SW Ecu-NW Arg.
<i>Oreotroch. estella</i>	++OH	Peru-Bol.	<i>Cnemarcus erythro.</i>	*-HF patchy Ven-Bol.
<i>O. adela</i>	++S	Cochabamba	<i>Polioxolmis rufipenn.</i>	*(O) Peru-Bol.
<i>Patagona gigas</i>	++S	Ecu-W Arg.	<i>Agriornis montana</i>	+OH S Col-S Arg.
<i>Aglaeac.cupri.</i>	++W-HF	Col-Peru	<i>A. andicola</i>	*-OH rare Ecu-NW Arg.
<i>A. castelnaud.</i>	* or ++W	Apurímac	<i>Notiochelidon murina</i>	*-Pa Ven-N Bol.
<i>Lesbia victoriae</i>	+S-W	Col-Peru	<i>N. flavipes</i>	+Pa-HF Ven-N Bol.
<i>L. nuna</i>	++S	Col-N Bol.	<i>Troglodytes aedon</i>	++U Americas
<i>Sappho sparganura</i>	++S-W	Bol-W Arg.	<i>Turdus fuscator</i>	+W-HF Ven-N Bol.
<i>Metallura phoebe</i>	++S-W	W Peru	<i>T. chiguanco</i>	++OH Ecu-W Arg.
<i>Metallura baroni</i>	* or ++W	Azuay, Ecu.	<i>Myioborus brunniceps</i>	+HF-W Bol-NW Arg.
<i>Chalcostigma stanleyi</i>	*-Pa	Ecu-N Bol.	<i>Conirostrum cinereum</i>	++U S Col- N Bol.
<i>Ch. olivaceum</i>	+OH	C.Blanca+Real	<i>C. tamarugense</i>	*(S) S Peru/N Chile
<i>Ch. heteropogon</i>	++Pa	Ven-Col.	<i>C. ferrugineiventre</i>	++HF C Peru-N Bol.
<i>Ch. herrani</i>	++Pa	Col-N Peru	<i>C. sitticolor</i>	+Pa-HF Ven-N Bol.
<i>Oreonympha nobilis</i>	+S-W	Apurímac	<i>Oreomanes fraseri</i>	** S Col-Bol.
<i>Veniliornis nigriceps</i>	+HF	Col-N Bol.	<i>Diglossa brunneivent.</i>	++S (Col.)Peru-N Bol.
<i>V. fumigatus</i>	+HF	Andean HF	<i>D. carbonaria</i>	++S Cochabamba
<i>Colaptes atricollis</i>	+W	W Peru-Marañón	<i>Xenodacnis parina</i>	*(HF) (Ecu.) Peru
<i>C. rupicola</i>	++OH	Peru-AW Arg.	<i>Thraupis bonariensis</i>	++S Ecu-Arg.
<i>Upucerthia serrana</i>	*	NW Peru	<i>Thlypopsis ruficeps</i>	+S-HF C Peru-NW Arg.
<i>U. andaecola</i>	++S	Bol-NW Arg.	<i>Saltator aurantii.</i>	+W-S Peru-Arg.
<i>U. ruficauda</i>	+S-O	S Peru-Arg.	<i>S. rufiventris</i>	*-HF Cochabamba
<i>Cincl. (exc.) aricomae</i>	**	Abancay-C.Real	<i>Catamenia inornata</i>	+S Ven-W Arg.
<i>Leptasthenura andic.</i>	H*OPa	Ven-NW Bol.	<i>Phrygilus atriceps</i>	*-OH SW Peru-NW Arg.
<i>L. striata</i>	*-S	S W Peru	<i>P. punensis</i>	+OH Peru-NW Bol.
<i>L. pileata</i>	*-W	N and W Peru	<i>P. fruticeti</i>	++S Peru-S Arg.
<i>L. xenothorax</i>	**	Abancay-Cuzco	<i>P. unicolor</i>	*-OH Ven-S Arg.
<i>L. (aegi.) berlepschi</i>	+OH	W Bol.	<i>P. plebejus</i>	+OH-S Ecu-W Arg.
<i>L. fuliginiceps</i>	++S	Bol-NW Arg.	<i>Atlapetes rufinucha</i>	+HF Col-N Bol.
<i>L. yanacensis</i>	**(Bol:*S)	C.Blanca, Aban.	<i>A. fulviceps</i>	++HF Cochabamba
<i>Cranioleuca baroni</i>	*-W	N-NW Peru	<i>A. schistaceus</i>	+Pa-HF Ven-Ecu., C Peru
<i>C. albicapilla</i>	*-W	Apurímac	<i>A. rufigenis</i>	*-W C.Blanca + Apurímac
<i>Asth. (dorbisg.) semisp</i>	*(S,O)	SW Peru	<i>A. nationi</i>	++W-S SE Ecu-W Peru
<i>Asthenes pudibunda</i>	++S-W	W Peru	<i>Zonotrichia capensis</i>	+U Ven-S Arg.
<i>A. heterura</i>	++S	Cochabamba	<i>Poospiza boliviana</i>	+S Cochabamba
<i>A. ottonis</i>	++S-W	Apurímac	<i>P. alticola</i>	** C.Blanca
<i>A. virgata</i>	+Pa	C Peru	<i>P. hypochondria</i>	+S Bol-W Arg.
<i>A. urubambense</i>	*-Pa	E ridge Peru-Bol.	<i>P. rubecula</i>	++W-S W Peru
<i>Phacell. striaticeps</i>	*-SW	C Peru/NW Arg.	<i>P. caesar</i>	++W-S Apurímac
<i>Grallaria andicola</i>	*(Pa)	Peru	<i>P. baeri</i>	*(S) Tucumán
<i>Scytalopus magellan.</i>	++PaW	in Peru part	<i>P. garleppi</i>	*(S) Cochabamba
<i>Acropternis orthonyx</i>	*-HF	Ven-N Peru	<i>Carduelis crassirostris</i>	** Peru-NW Arg.
<i>Ampelion rubrocrist.</i>	+W-HF	Ven-Bol.	<i>C. magellanica</i>	+S-W Col-Arg.
<i>A. stresemanni</i>	*(W)	C.Blanca-Lima	<i>C. atrata</i>	*-OH Peru-NW Arg.
<i>Mecocerc. leucophrys</i>	+HF	Andean HF	<i>C. uropygialis</i>	+O-S W Peru-Chile-Arg.

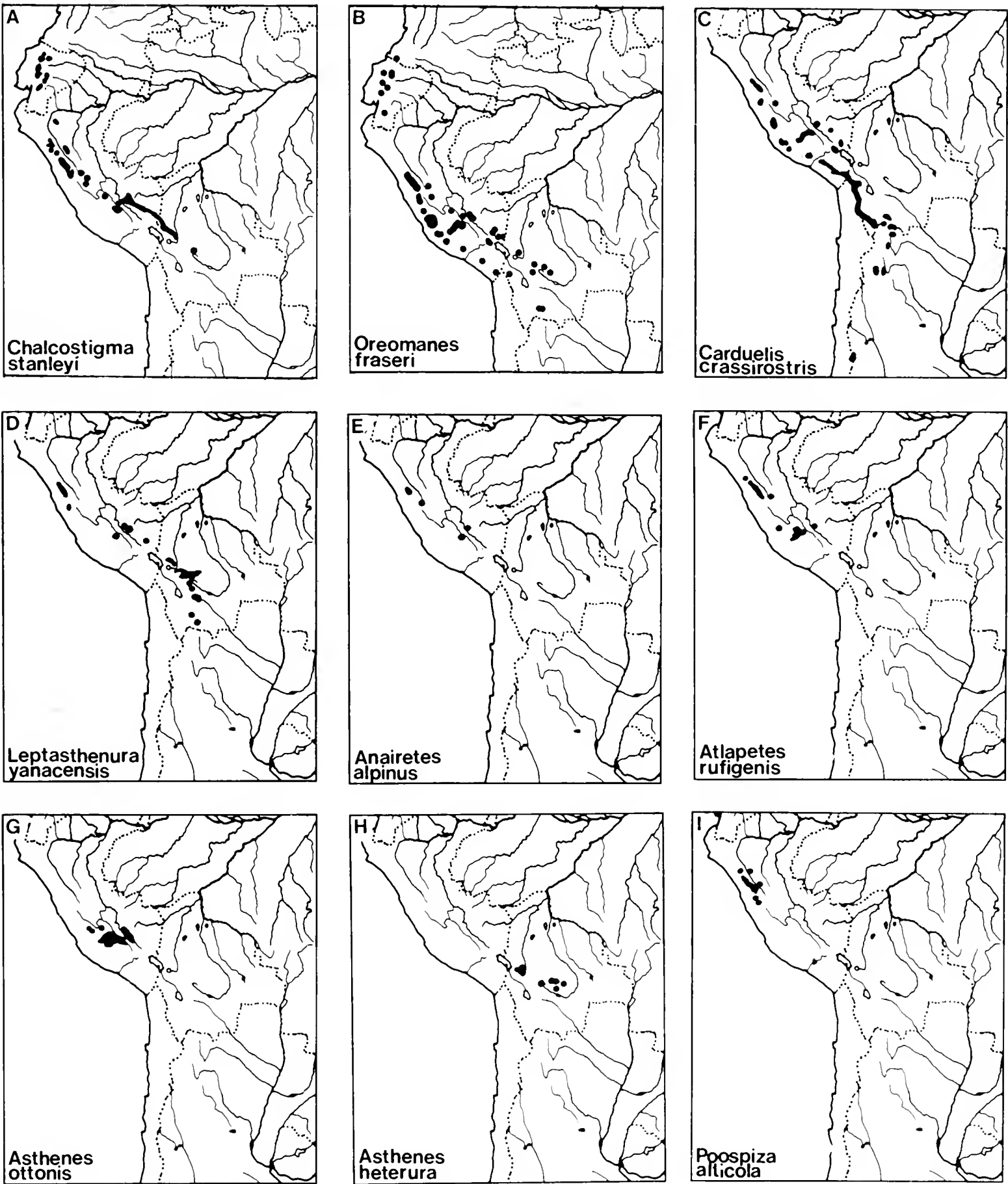


FIGURE 2 - Three examples of distributions (adapted from Fjeldså & Krabbe 1990). Wide-spread but patchy species (A-C), disjunct species (D-F), and endemic species with restricted distribution (G-I).

marginal habitat for species of lower-elevation humid forest or paramo habitat. *Oreomanes fraseri***, the only genuine *Polylepis* bird in this area, may have come from Peru (Figure 2b). Since the patches of high-elevation woodland in the northern Andes, always in proximity of lower-elevation forest, apparently lack specialists, this area is excluded from further analysis.

Some *Polylepis* specialists are almost as widespread as the fragmented habitat itself (*Polioxolmis rufipennis**, *Ochthoeca oenanthoides**, *Oreomanes fraseri***, *Carduelis crassirostris***); compare Figures 2 and 3), which obscures their biogeographic origin. *Oreomanes* may be perfectly adapted for surviving in small populations far away from lower-elevation refuge habitat. Other species maintain a wide range by wandering in the non-breeding season. Other species and megasubspecies have more restricted ranges, some being endemic to a small area (Figure 2).

SUBCENTERS IN THE WEST CORDILLERA. Many species occur along almost the entire West Peruvian Andean Subcenter (Cracraft 1985), but others are more local (see density peaks in Figure 3a). The highest concentration of endemic species is in semihumid canyons from the Cordillera Blanca draining into the headwaters of the Río Marañón. This subcenter is squeezed between a center of endemism on the upper Pacific slope of Lima, and one in the upper Marañón valley, with endemics both in the arid subtropical part (Cracraft 1985) and in temperate scrub in side valleys. The C. Blanca and Lima subcenters are connected by mountain chains which have *Polypelis* patches scattered almost all the way to Oyón in northern Lima. *Upucerthia serrana**, *Ampelion stresemanni**, *Xenodacnis parina petersi*** and *bella** and *Poospiza rubecula** span both subcenters. However, megasubspecies *pallidior** of *Mecocerculus leucophrys*, *Anairetes nigrocristatus*, *Atlapetes r. rufigenis** and *Poospiza alticola*** are centered in C. Blanca; *Leptasthenura striata**, *Anairetes reguloides* and *Atlapetes nationi/seebohmi* are centered on the Pacific Slope. Strong differentiation of C. Blanca

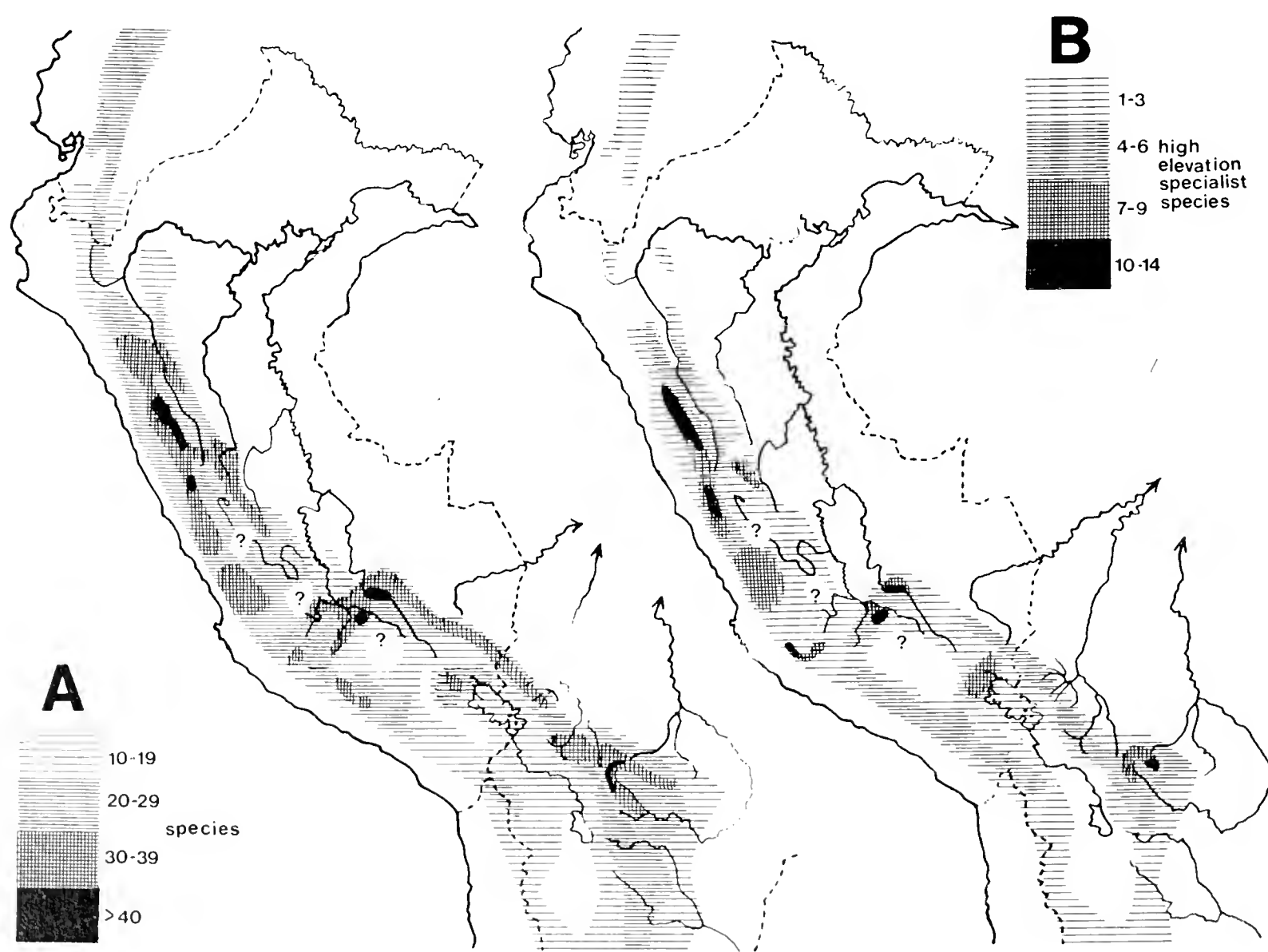


FIGURE 3 - Density of species living in *Polylepis* woodlands (all Table 1 species, A), and of high-elevation specialists (starred in Table 1, B).

centered and Lima-centered subspecies of *Leptasthenura pileata** and *Cranioleuca baroni**, and weak differentiation in some other species, suggest periods of past isolation. Some racial shifts also exist further south, and to this can be added an unnamed semispecies* of the *Asthenes dorbignyi* group (see Fjeldså & Krabbe 1990:365-70) and *Conirostrum tamarugense*.

THE APURÍMAC CENTER. Many species are centered in the Andahuaylas-Abancay area in Apurímac, but three of these range as far south as Puno, in tiny rainshadow areas within the Cordillera Real. High-elevation endemics are *Nothoprocta taczanowskii*, *Aglaeactis castelnaudii**, *Oreonympha nobilis*, *Asthenes ottonis* and *virgata*, *Cranioleuca albicapilla**, an unnamed *Scytalopus*, *Xenodacnis p.parina**, *Atlapetes rufigenis forbesi** and *Poospiza caesar*. Four of these show slight to well-marked subspecific differentiation within this range. The species inhabit patches of semihumid woodlands on the edge of the puna in otherwise arid valleys, but *A. virgata* is typical of páramo/*Polylepis* ecotones across central Peru.

The Apurímac center was not recognized by Cracraft (1985), who pooled most of its species with the humid-forest birds of an East Peruvian Andes Subcenter, but two with humid-forest forms in the South Peruvian Subcenter. *Cinclodes (excelsior) aricomae*** and *Leptasthenura xenothorax*** of his South Peruvian Subcenter have tiny populations in C. Real and southeast of Abancay (Fjeldså & Krabbe 1990:846-7).

COCHABAMBA CENTER. The intermontane basin of Cochabamba is the center for *Oreotrochilus adela*, *Asthenes heterura*, *Diglossa carbonaria*, *Saltator rufiventris**, *Atlapetes fulviceps*, *Poospiza boliviana* and *garleppi** (other endemics inhabiting open habitat or lower-elevation forest). Some of these extend south to the Andean scarp of northern Argentina.

Surprisingly Cracraft (1985) did not treat Cochabamba as an area of endemism, but pooled its species with the Austral Andean Center, and one species in the South Peruvian Andean Subcenter. The situation is in fact complex. Besides Cochabamba endemics, other taxa are differentiated in Bolivian and Argentine semispecies. *Sappho sparganura*, *Upucerthia andaecola* and *Leptasthenura fulviceps* span both centres. There is probably an independent center for birds of prepuna and arid puna on adjacent altiplanos.

Relationships between faunas

LESSONS FROM TRACKS CONNECTING WELL DIFFERENTIATED TAXA. Of the seven widespread *Polylepis* specialists (Table 1), five have their closest relative in the humid montane forest. Most of these relatives are widespread along the east Andean slope, but *Cnemarchus erythropygius** (related to *Polioxolmis rufipennis**) is rare and local, and *Conirostrum ferrugineiventre* (possibly related to *Oreomanes fraseri***) is disjunct (east slope of central Peru and from Cuzco to Cochabamba). *Carduelis magellanicus* ("ancestor" of *C. crassirostris***), is widespread, but is absent from the arid puna of northern Chile, where *C. crassirostris*** may have originated in isolation in the *Polylepis* zone above the Atacama desert. The last species of this widespread group (*Leptasthenura andicola**) belongs in a group of southern origin.

More narrowly distributed endemic species show various faunal connections. Some tracks connect the West Andean Subcenter or parts of this subcenter with Apurímac, or the Bolivian slopes, and connect this latter area with adjacent lowlands. Among

Oreotrochilus hummingbirds, the Cochabamba form *adela* seems more primitive than its higher-elevation congeners. A close C. Blanca-Apurímac relationship is shown for the megasubspecies of *Atlapetes rufigenis**, and a close Apurímac-Cochabamba relationship for *Asthenes ottonis/heterura*.

Some strange long-distance relationships exist also: *Oreonympha nobilis* (Apurímac) apparently is the sister taxon of *Oxypogon guerinii* (Colombia); *Cinclodes (excelsior) aricomae*** (Abancay-C. Real) is the sister taxon of *C. excelsior* spp. of Ecuador-Colombia.

Most specialists live characteristically well isolated from the ranges of nearest lower-elevation taxa, or overlap only marginally. No *Polylepis* specialist for which the East Cordillera seems to be optimal has a close relative in the adjacent zone of humid forest. *Asthenes urubambensis**, restricted to the east Andean treeline ecotone has its nearest relative (*Asthenes flammulata* group*) patchily distributed on higher elevations. Thus *A. urubambensis** has adapted to this ecotone habitat from above rather than from below.

INTERPRETATIONS BASED ON SPECIFIC PHYLOGENETIC HYPOTHESES. The fact that few *Polylepis* specialists form superspecies or species groups (Table 1) suggests that much of this fauna arose by independent events with little subsequent opportunity for speciation. A few exceptions exist, though.

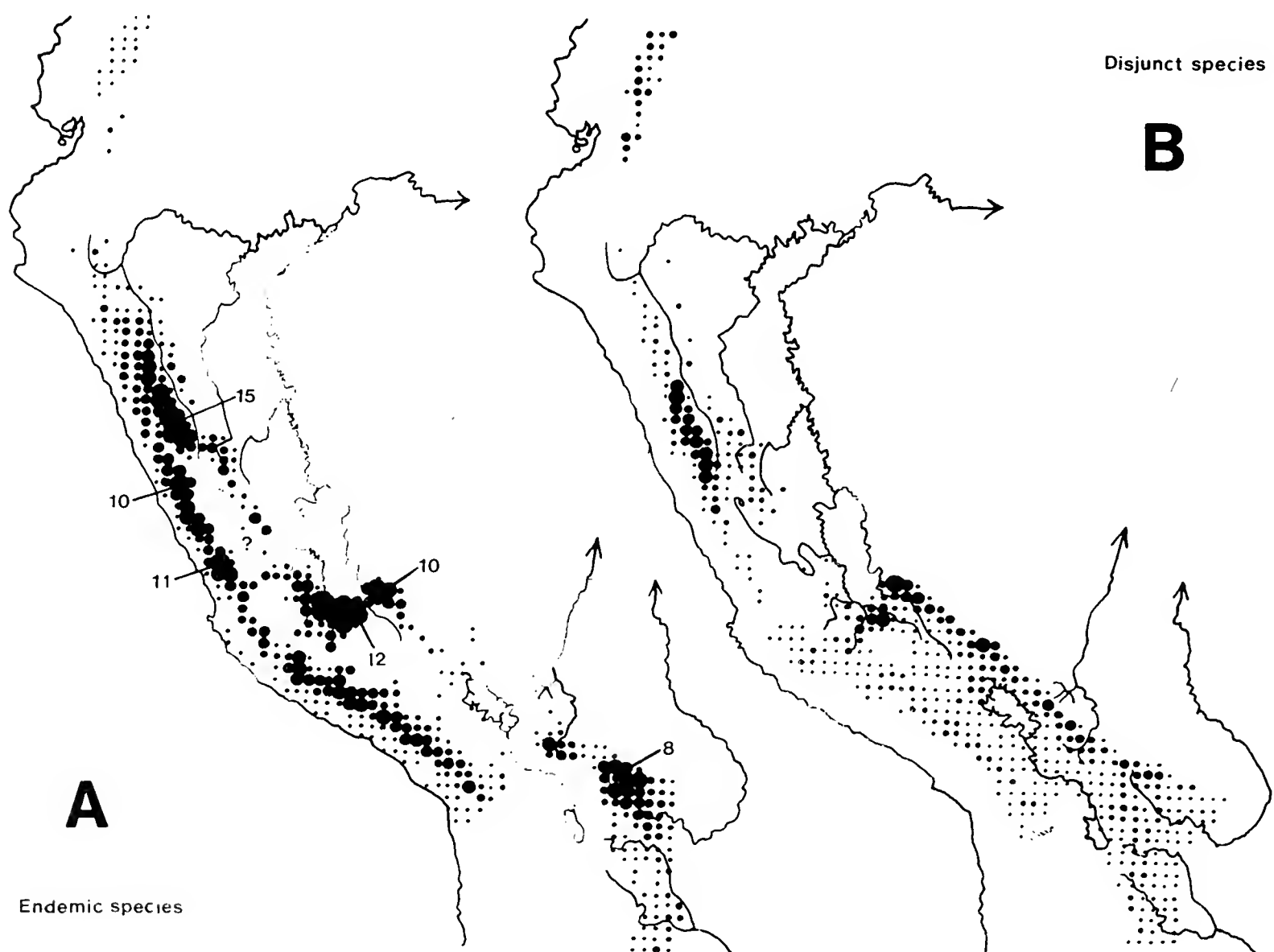


FIGURE 4 - Density of endemic species with restricted distributions, and of megasubspecies found in *Polylepis* woodlands (A) and of *Polylepis* species having disjunct populations (B).

Leptasthenura spinetails (Figure 5a) apparently originated in Argentina or southern Brazil, two groups invading the highlands. Possibly *L. yanacensis* arose early by isolation in Cochabamba, and then spread north, its Peruvian populations** becoming narrowly attached to *Polylepis*. The other group may have ascended via the southern "monte" and "pre-puna" habitats and speciated in Peru after having first adapted to Andean shrubsteppe and *Polylepis*. The three top branches(*-**) of the phylogeny can clearly be interpreted in terms of isolation on the Pacific slope of Peru, subsequent isolation in the north, and finally colonization to mountains of Apurímac/Cuzco.

Atlapetes brushfinches are typical of humid Andean forest. One branch (Figure 5b) possibly crossed the North Peru Low and became isolated in pockets of semihumid habitat on the Pacific slope, one clade spreading south in western Peru, in part in *Polylepis*. One population then became isolated on the Marañón slope of C. Blanca (*A. r. rufigenis**; with secondary contact and casual hybridization with *A. (nationi) seebohmi* in Cajamarca) and subsequent spread to Apurímac (*A. r. forbesi**).

The warblingfinches, *Poospiza*, are confusing, and my phylogeny (Figure 4c) is tentative and unrooted. This group clearly radiated in the lowlands of Argentina and Bolivia, but two clades adapted to highland conditions occur as far as C. Blanca.

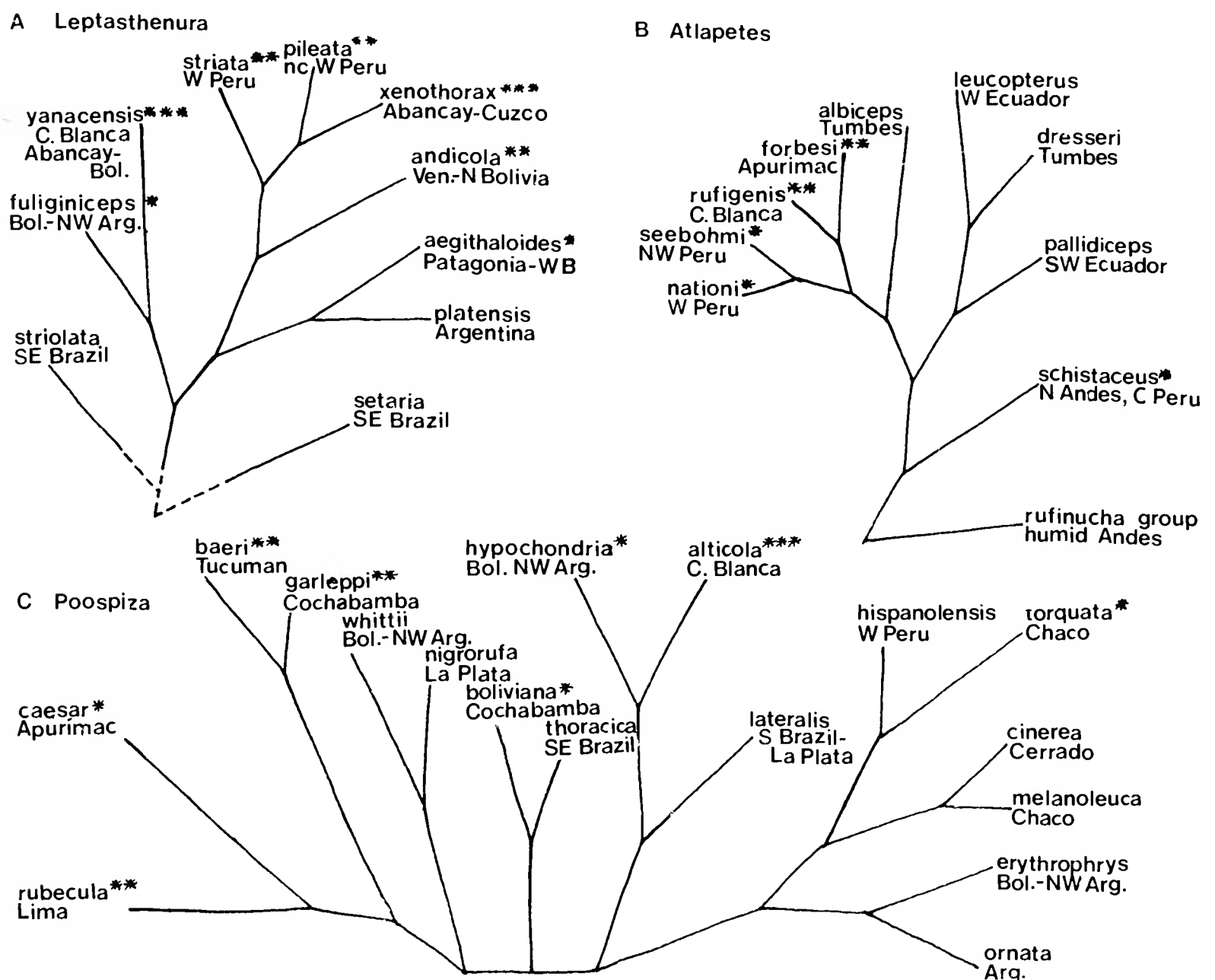


FIGURE 5 - Phylogenetic hypotheses for *Leptasthenura* spinetails (A), the *Atlapetes* *schistaceous* group of brushfinches (B) and *Poospiza* warblingfinches (C). One to three asterisks (*) indicate increasing association with *Polylepis*.

DISJUNCT DISTRIBUTIONS SUGGESTING YOUNG RANGE FRAGMENTATIONS. Many species inhabit widely separated areas (Figures 2d-f and 4b). Since the populations are weakly differentiated a fairly recent range fragmentation can be inferred. For birds of *Polylepis* near the humid treeline ecotone, breaks have taken place mainly between Ecuador and Peru, and between C. Blanca-adjacent Pasco and Abancay-C. Real. This southern gap consists of low ridges with limited cloud-cover interrupted by many dry valleys. These ridges may be poor for these birds.

Cycles of dispersal and range fragmentation in central Peru can be invoked to explain the differentiation of two megasubspecies of *Xenodacnis parina**, and of *Chalcostigma stanleyi** and *olivaceum*, now partly sympatric.

For birds of semiarid wood/scrub, range disjunctions exist along the Pacific slope and toward small populations in the valleys of Huancavelica-Ayacucho and the Titicaca basin. Remnants of a track from Cochabamba to central Peru can be seen for *Phacellodomus striaticeps*. This species inhabits xerophytic thickets in the lower temperate zone from northern Argentina to La Paz (*striaticeps*) and in valleys of Cuzco-Apurímac (*griseipectus*). An unnamed subspecies* inhabits a large *Polylepis* woodland near Lampa (Lake Titicaca area).

LESSONS FROM CURRENT DISPERSAL. Distribution details showing how species locally expand out of their normal life-zone to enter another may exemplify how dynamic biogeographic changes could have happened in the past:

Many lowland species of arid woodland as well as humid shrub enter the Cochabamba basin, reaching the *Polylepis* woodlands or almost the puna edge. I suggest that the mosaic of rainshadows and moisture-capturing ridges, together with the expected rise in temperatures in rainshadow areas, create opportunities for lowland birds of various ecological requirements to use Bolivian valleys as gates to the highlands. Some of the Cochabamba populations are differentiated as subspecies, so we are not watching effects of man-made habitat changes.

In Apurímac, some of the more adaptable humid-forest birds colonize *Polylepis*-dotted scarps fringing arid valleys (e.g., *Ampelion rubrocristatus*). Distributional data also show some exchange of species across the pass between Huánuco and the Upper Marañón C. Blanca (Figure 3a) or over to northern Lima (isolated populations of *Coeligana violifer*, *Pterophanes cyanoptera* and *Pipraeidea melanonota*).

Humid-forest birds like *Veniliornis fumigatus* and *Basileuterus nigrocristatus* occur above 4000 m in C. Blanca. Similar colonizations may also have taken place long ago, judging from the presence here of a highland megasubspecies* of the widespread humid-forest *Mecocerculus leucophrys*.

Many birds of the arid Pacific slope make considerable vertical movements, seasonally or in response to an el niño cycle. Isolated populations of some west slope birds in some arid, east-draining valleys suggest crossings of the West Cordillera in north Peru, in C. Blanca (where *Colaptes atricollis* lives above 4000 m) and from the Rio Cañete drainage in southern Lima.

The high-elevation birds *Grallaria andicola** and *Xenodacnis p.parina** colonize humid treeline habitat in the eastern Andes.

CONCLUSIONS

Correlations of areas of endemism can be used to corroborate or falsify hypotheses about patterns of dispersal. In the present case the suggested routes are in good agreement with current patterns of dispersal, suggesting that biogeographic processes operating today also did so, periodically, in the past. An important track went from the foothills in Bolivia to Cochabamba, and then across the Altiplano to the Pacific slope of Peru, or to Apurímac and from there to C. Blanca and Lima. Also, dispersal of birds of humid montane forest to C. Blanca and the Pacific slope of northern Peru is important, and may have happened in the distant past judging from the fact that most specialized (old) *Polylepis* birds have their counterparts on the humid eastern Andean slope. After specializing to high elevation woodlands they may have had periodic opportunities to disperse from C. Blanca to Abancay-C. Real along the humid eastern ecotone (Figure 3b), and to speciate after range interruption. However, only part of the speciations share geographic histories, other events being unique, as species have used a number of different ways to colonize high-elevation woods.

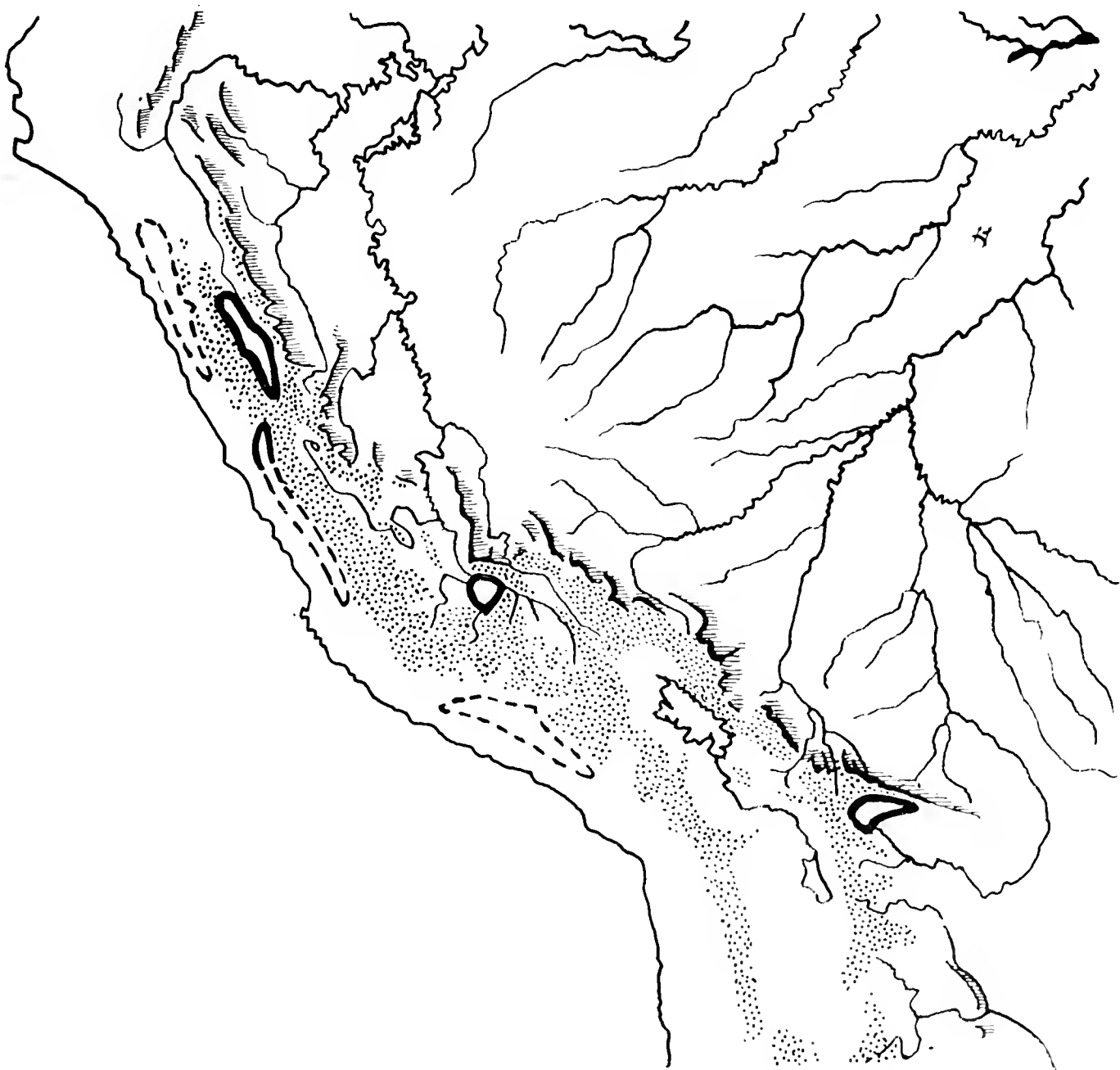


FIGURE 6 - Hypothesized species-generating areas. Stippled is maximum area of Pleistocene glaciers. East-facing slopes that may have remained wooded are shaded.

Many species of Andean valleys and slopes, endemic and widespread forms alike, ascend to *Polylepis* on scarps toward adjacent highlands, but apparently this situation at the margin of the ecological range does not give the break in geneflow necessary for specialization. Specializations to highest-elevation woodlands are shown only by forms living far from the possible founding areas (or in part living far away, permitting the interpretation that proximity is secondary). This pattern suggests that the specialization was allopatric rather than peripatric. (However, restriction to high elevation habitat could be reinforced by successive colonizations of an area, because of competitive interaction from the more recent colonizer, as in *Aglaeactis cupripennis/castelnaudii** and *Metallura williamilbaroni**, see Fjeldså & Krabbe 1990: 258 and 282).

I postulate that specialization to high-elevation woodland required interruption of geneflow with lower-elevation stocks, especially if opportunities to spread from the humid East Andean slope to C. Blanca or Lima were followed by habitat contraction. Isolated on the Pacific slope, these birds found the most permanently humid habitat in the *Polylepis* zone. A few species also arrived at the Pacific slope from the scrubby valleys of Bolivia directly across the altiplano or via Apurímac. Incipient specialization to *Polylepis* could have been reinforced by periods of isolation in *Polylepis* woodland on the altiplano, far from Andean slopes and valleys (Vuilleumier 1986). The pattern of endemism does not support the view that woodland birds survived glacial periods in ice-free refugia around Lake Junín (Fjeldså 1981, Hansen et al. 1984) and on the altiplano (Simpson 1975, Servant & Fontes 1978).

The suggested patterns fit well with the assumed Pleistocene cycles of contraction and expansion of forest habitat (Simpson & Haffer 1978, Flenley 1979, Prance 1982). When discussing potential Pleistocene refugia it is worth mentioning the topographic situation of C. Blanca, the Abancay area and the Cochabamba basin (Figure 6). All are isolated by mountain ranges from the humid slopes, but sufficiently close for some rainfall from the clouds that often surround the snow-covered peaks at the headwaters of the Marañón, where the Apurímac Canyon intersects the highland north of Abancay, and in the Tunari Range isolating the Cochabamba basin. Because of positive effects of glaciers on the climate in immediately adjacent refuge areas (Lindroth 1965), and large past wetlands in the Cochabamba basin, these areas are likely to have maintained some woodland throughout the glacial cycles and have entrapped populations of a variety of once-widespread forms, thus generating new species. Steep elevational gradients from the cool and humid zone near the glaciers to the hot and arid climate at the bottom of rain-shadow valleys would permit wide adaptational diversity in these refuges. Subsequently, lower-elevation endemics could spread through the montane valley, while *Polylepis* specialists could follow moisture-capturing ridges across central Peru or pass from Abancay to C. Real. Simpson (1975) suggests the presence of a *Polylepis* zone on the Pacific slope of Peru during the glacial periods.

It is hard to accept Cracraft's (1985) view that present areas of endemism are discrete pre-Pleistocene units inhabited by subspecies and species alike, irrespective of habitat, as opposed to "refuges". The attempt is weakened by his above-mentioned inaccuracies when allocating species to specific areas. Nevertheless, the hypothesis of speciation resulting from Pleistocene climatic cycles needs testing using "molecular evolutionary clocks" such as DNA base-sequencing, predicting that Pleistocene cycles should result in rather constant nodal distances across several species groups.

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CONCLUDING REMARKS: BIOGEOGRAPHY AND SPECIATION IN NEOTROPICAL BIRDS

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INTRODUCTION

The papers in this symposium cover the Neotropics from its northern limit (Escalante) to its southern extremity (Vuilleumier), including its main mountain system (Franke, Fjeldså), and its largest river (Capparella). These papers also offer several approaches to biogeography and speciation. Thus, emphasis varies from consideration of a single taxon (*Geothlypis*), to analysis of an entire fauna (Patagonia). Ecologically, the habitats represented include open vegetation, lowland rainforests, and montane woodlands. The geographical focus on the high altitude woodlands is either specific (Peru) or general (tropical Andes). Finally, a single question is treated in the case of Amazonia, whether rivers of this basin act as barriers. The diversity of biological questions and of research strategies used in these papers reflects the ecological, taxonomical, and evolutionary diversity of the Neotropical Region itself.

HOW MUCH IS BEING DONE

The sample of research provided in this symposium shows the degree of detail pursued today. At the local level, Franke has surveyed dozens of dry cloud forest patches along the western Andes of Peru, whereas at the global level Fjeldså has explored dozens of relictual woodlands over the entire length of the tropical Andes. Key taxa have been assayed with electrophoresis for a better understanding of population structure in areas as different as Baja California (Escalante) and the heart of Amazonia (Capparella). And parapatric contacts between sister taxa are studied at the southernmost tip of the region (Vuilleumier).

HOW MUCH REMAINS TO BE DONE

With such a vast region and such a rich fauna, there is almost no end to the number of questions that need answering. The authors of these papers point out specific avenues for future work. Thus Capparella urges the use of biochemical data for a better assessment of areas that should be protected in Amazonia. The practical application of scientific results from speciation analysis to conservation cannot be more clear. On a more academic level, Capparella's research shows the need for more paleoecological data in lowland rainforests, so that better correlations can be made between history inferred from electrophoretic information and history inferred from dated sequences of fossil pollen.

Franke's work emphasizes the need for good, well labeled series of specimens from many localities in order to make accurate assessments of detailed distribution patterns. Vuilleumier's review reveals the uniqueness of the Patagonian avifauna. Southernmost South America appears to be both a diversity sink (relict taxa) and a diversity generator (vicariance in situ). Escalante makes tantalizing suggestions about fine grained differences between warblers that live in wetlands and others that live in drier habitats. In spite of hard work, still larger samples will be needed before one can elucidate the switch from marsh to non-marsh in *Geothlypis*. Fjeldså mentions taxa that can be singled out for study of colonization of relict woodlands at very high altitudes in the Andes.

CONCEPTUAL ADVANCES

At the XVIIth IOC in Berlin, Short convened a symposium on speciation in South American birds, with papers on upper Amazonia, the high Andes, suboscine versus oscine radiation, woodpecker speciation, and flycatcher speciation. Geographically the present symposium reveals a finer level of analysis than the one in Berlin. Methodologically, the blend of morphological, ecological, and biochemical kinds of evidence is now routine in the Neotropics. The liquid nitrogen tank is today a standard piece of equipment in expeditions. What about conceptual advances provided by this more versatile approach?

In terms of the refuge theory, I worry that the advances made by paleobotanists, such as those discussed by Huntley (1988) and Webb (1988) at the 19th IOC in Ottawa, have not yet been incorporated by ornithologists in their daily thinking.

In terms of geographical ecology we have made good progress away from a quasi-typological thinking focused on subspecies (embodied in Zimmer's work on geographical variation in birds from the Peruvian Andes), as is evident when reading Franke's paper. Subspecies are a tool for distributional analysis, no longer an end in themselves.

In terms of speciation, many more cases have been studied since the 1978 IOC in Berlin. Hence research on the course of speciation (Vuilleumier 1980) has progressed to the point where enough taxa have now been analyzed, and from so many more areas of the Neotropics, that one can see at once, and in much richer detail, both the unity of the process in different taxa and different areas, and the diversity of its development. Nevertheless, more research is needed on parapatric taxa, in order to sort out the confusing array of potential causal factors that have produced parapatry. In other words, we have not yet obtained enough evidence to fully refute Endler's (1982) claims that at least some parapatric patterns could be the result of speciation along clines that are or were parallel to environmental gradients.

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SYMPOSIUM 2

**ORIGINS AND EVOLUTION OF THE
AUSTRALASIAN AVIFAUNA**

Conveners R. SCHODDE and L. CHRISTIDIS

SYMPOSIUM 2

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INTRODUCTORY REMARKS: ORIGINS AND EVOLUTION OF THE AUSTRALASIAN AVIFAUNA

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Zoogeographically, Australasia stretches from Sulawesi in the west to the Hawaiian Islands and Easter Island in the east. Its limits are not clear-cut and the boundary between the Australasian and Oriental regions has not been resolved conclusively, perhaps because it cannot be. The geological history of the boundary is complex, with Sulawesi formed from both Gondwanan (eastern half) and Eurasian (western half) elements (Audley-Charles 1981). The habitats of Australasia cover the whole range of global environments, from semi-arid deserts to tropical rainforests, alpine grasslands and temperate scleromorphic forests. These are interspersed amongst continental land masses, volcanic islands and islands which are part of continental plates. All these factors combined have produced in Australasia a very rich and unique avifauna, with a greater species diversity per area than any other zoogeographical region. Over 90 percent of the land and freshwater bird species are unique to the region.

Not surprisingly, the Australasian avifauna - its origins and radiations - has continued to capture the attention of biologists since the time of A.R. Wallace. Considerable interest and controversy has centred on the relationships of the land bird fauna. Traditional theory has had it that Australasia received its avifauna through a series of successive waves of immigration from Eurasia over the last 30 to 40 million years (Keast 1984). Advances in plate tectonics, paleontology and molecular biology have challenged this view. The timing of continental drift has revealed that when Australia was supposed to be getting its early stocks of Eurasian birds, it was in fact thousands of kilometres further south towards Antarctica (Rich 1975). Moreover, fossil evidence demonstrates the presence of birds in Australia 110 MYBP and passerines at least 30 MYBP (Rich and Baird 1986). These facts have led to the conclusions that some of the major orders of birds are Gondwanan in origin. Which groups are Gondwanan, however, is still some way from final resolution (Olson 1988).

By far the greatest controversy centres around the molecular data from DNA-DNA hybridization (Sibley & Ahlquist 1985). The results so far suggest that the Australasian passerines are autochthonous and have undergone marsupial-like radiations. The radiations themselves seem to be old, lending support to the view that the passerines originated in Gondwana.

The interest generated from these studies is reflected in the fact that the origins and subsequent radiations in the Australasian avifauna have been popular as subjects of symposia and papers at three of the last six International Ornithological Congresses. The venue of the 20th congress here in the Antipodes adds to the topicality of yet

another symposium on the subject, here drawing on its information from the following aspects: regional palaeogeographic history, the regional fossil record, molecular contributions on the origins of the passerines, adaptive radiations in the parrots and cockatoos, and the biogeographical history of regional avifaunal assemblages.

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GEOLOGICAL EVOLUTION AND BIOTIC LINKS IN THE MESOZOIC AND CENOZOIC OF THE SOUTHWEST PACIFIC

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ABSTRACT. From middle Jurassic times earth movements began to create considerable areas of land in the New Zealand region. By late Jurassic and early Cretaceous times, a large landmass had been developed, extending north towards New Caledonia, east to Chatham Islands, west to Lord Howe Rise and south to the edge of Campbell Plateau. Development of this landmass, and its associated terrestrial links, together with the warm-temperate conditions then apparent over large areas of Gondwana, provided favourable conditions for the spread of Gondwanan elements in the region. In early and middle Cretaceous Australia, New Zealand, New Caledonia and Antarctica were characterised by cool-temperate climates, and these regions shared many cool-temperate biotic elements; land links provided access and exchange for early angiosperms. However, all land links between New Zealand/New Caledonia and Australia/Antarctica were broken after 85 Ma. From this time onwards the ancestral Tasman Sea and Southern Ocean became effective barriers to overland dispersal between southeastern Gondwana and New Zealand/New Caledonia. Subsequently, and consequently all terrestrial colonists had to arrive by flying, swimming or floating. Many birds did so, but no terrestrial snakes and no mammals, except bats.

Keywords: Jurassic, Cretaceous, Cenozoic, Rangitata Orogeny, Gondwana, New Caledonia, Papua New Guinea, Australia, New Zealand, Antarctica, South America.

INTRODUCTION

Throughout early Mesozoic time immediately preceding the advent of birds, the SW Pacific region underwent a series of major changes in geography, climate and topography that set the scene for the biotic developments that took place in the late Mesozoic and Cenozoic. During this time, the major landmasses that now comprise the SW Pacific region (i.e. Australia, Antarctica, New Zealand and New Caledonia) were integral parts of the southeastern edge of the supercontinent Gondwana.

In Carboniferous and Permian times Gondwana had slowly drifted across the South Pole, and large areas of Australia and Antarctica had been scoured by continental ice sheets (McKerrow & Scotese 1990). During these times the areas now occupied by New Zealand and New Caledonia (then virtually one landmass) were largely under the sea, except for ephemeral volcanic islands, and as a consequence escaped the effects of glaciation (Stevens 1985).

During the Triassic the same global movements continued that had earlier rotated the continents of southeastern Gondwana towards the South Pole. However, in the Triassic these movements had the net effect of gradually moving southeastern Gondwana into mid-latitudes. Nonetheless, New Zealand (and New Caledonia) remained in high latitudes (70°-80°S) for much of Triassic time. But, as it is likely that the world was ice-free during the Triassic (Hallam 1985), New Zealand and New Caledonian climates were probably not colder than cool- or cold-temperate (Stevens 1980a, 1985).

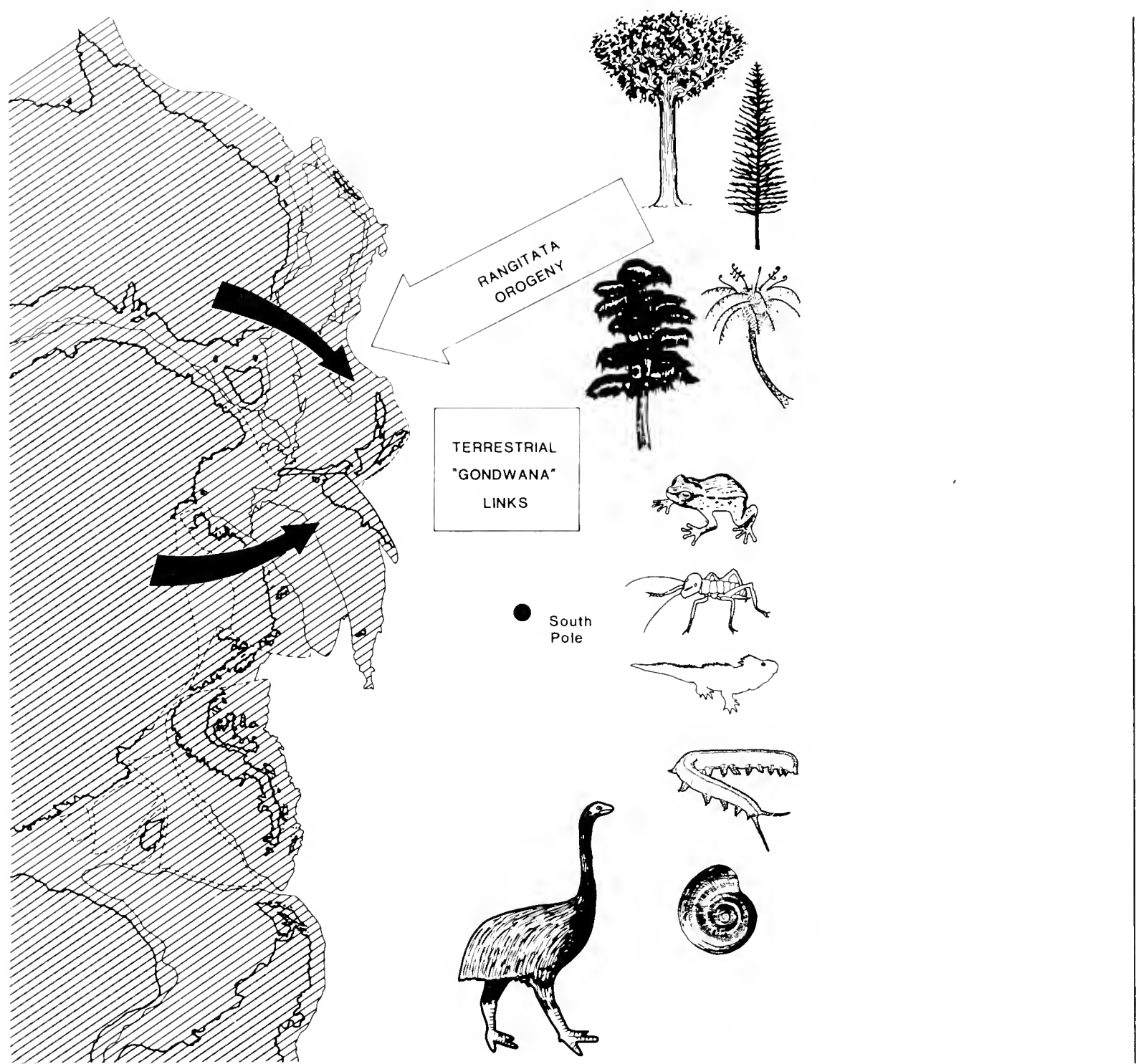


FIGURE 1 – Diagrammatic reconstruction of the southeastern margin of Gondwana in the middle and late Jurassic, ca. 165-145 Ma. Base map for this and the succeeding diagrams Figures 2-3 modified from Grunow, Dalziel & Kent (1987), Grunow, Kent & Dalziel (1987), Lawver & Scotese (1987), de Wit et al. (1988). The diagonal line pattern indicates regions in which extensive areas of land were present at the time, although its exact distribution is not known. At this time, movements of the Rangitata Orogeny were creating new land in the New Zealand region. Development of this new land provided opportunities for New Zealand to share in the terrestrial biota of adjacent Gondwana lands, as indicated by the solid arrows. Biota that populated New Zealand at this time (and perhaps also earlier in the Triassic, when land links were also present), included at least some of the ancestral stocks of the “archaic” elements present in the modern New Zealand flora and fauna. Representatives of such stocks are shown along the right hand edge of the diagram: (from top to bottom) the Kauri *Agathis australis* (araucarian stocks); podocarp stocks; tree-fern stocks; the New Zealand Frog *Leiopelma*; Weta *Deinacrida heteracantha* (Rhaphidophoridae), Tuatara *Sphenodon punctatus*; *Peripatus*; the giant New Zealand Land Snail *Paryphanta*. Ratite birds, including the ancestors of the New Zealand Moa (Dinornithiformes) may also have populated Gondwana lands at this time, assuming that walking rather than flying was their preferred mode of locomotion. The boxes highlight the factors (e.g. “Rangitata Orogeny”) that influenced biotic developments in the New Zealand region at the times covered by the reconstructions.

The Triassic saw a carry-over of the general sedimentary conditions of the Permian, with much of New Zealand and New Caledonia continuing to be sites of active island arc systems, flanking the coastline of southeastern Gondwana. However, judging from sequences of non-marine beds, there was probably more land present in New Zealand and New Caledonia in the Triassic than in the Permian (Stevens & Suggate 1978, Retallack 1987). The new land areas that developed may have established more permanent land links to southeastern Gondwana (in contrast to the probably more ephemeral links of the Permian), and provided access for ancestral plant stocks, including ancestors of groups such as psilotales, ferns, lycopods, araucarians, podocarps and ginkgos (Fleming 1975, p. 10, 1977a, 1978).

JURASSIC

Rotation of eastern Gondwana in a direction away from the South Pole continued in the Jurassic, changing New Zealand's geographical position to 60°-70°S by middle Jurassic times (Stevens 1980a, 1985). As a result of the progressive movement of land away from the polar regions, world climates continued to improve, and consequently, Jurassic climates were appreciably more equable than those of the present day (Stevens 1980a, Hallam 1975, 1985, Frakes 1986).

Evolution of Greater New Zealand

Throughout Jurassic times the earth movements of the Rangitata Orogeny, the initial stirrings of which were evident in the middle and late Triassic, became even more marked (Fleming 1967a, 1970, Stevens 1978, Suggate, 1978, Bradshaw et al. 1981). These movements progressively folded and elevated above sea level much of the material that had been deposited in the basin structures of the Carboniferous/Triassic arcs in the New Zealand - New Caledonian region. By the middle Jurassic, and extending into the earliest Cretaceous, a large new landmass had developed, which extended far beyond the shorelines of modern New Zealand: northwards at least as far as New Caledonia, westwards to the Lord Howe Rise; eastwards to the Chatham Islands; and southwards to the southern edge of the Campbell Plateau (Figure 1). As rifting had not yet begun on what was to become the site of the Tasman Sea and Southern Ocean, such a landmass was virtually continuous with Australia and Antarctica, which at that time were largely emergent (e.g. Storey et al., 1987, St. John 1984, White 1986). Long fingers of land and interlinked chains of islands probably also extended northwards from the new landmass towards Papua New Guinea and Indonesia, although exactly how far is not known. The formation of such large areas of land in the middle/late Jurassic and earliest Cretaceous probably constituted the greatest development of new land that ever occurred in the New Zealand region.

Dispersal of "archaic" biotic elements to New Zealand

Development of "Greater New Zealand" and its links with the lands of southeastern Gondwana, when taken together with the equable climatic conditions that were then widespread, provided optimal opportunities for the spread of terrestrial organisms. At this time, the ancestors of many of the "archaic" elements present in the modern New Zealand terrestrial biota became established assuming that their stocks had originally developed in other areas. Among plants, these ancestral stocks may have included araucarians and podocarps, following on from the Triassic. Among animals, ancestral stocks of at least some of the following became established in New Zealand in the

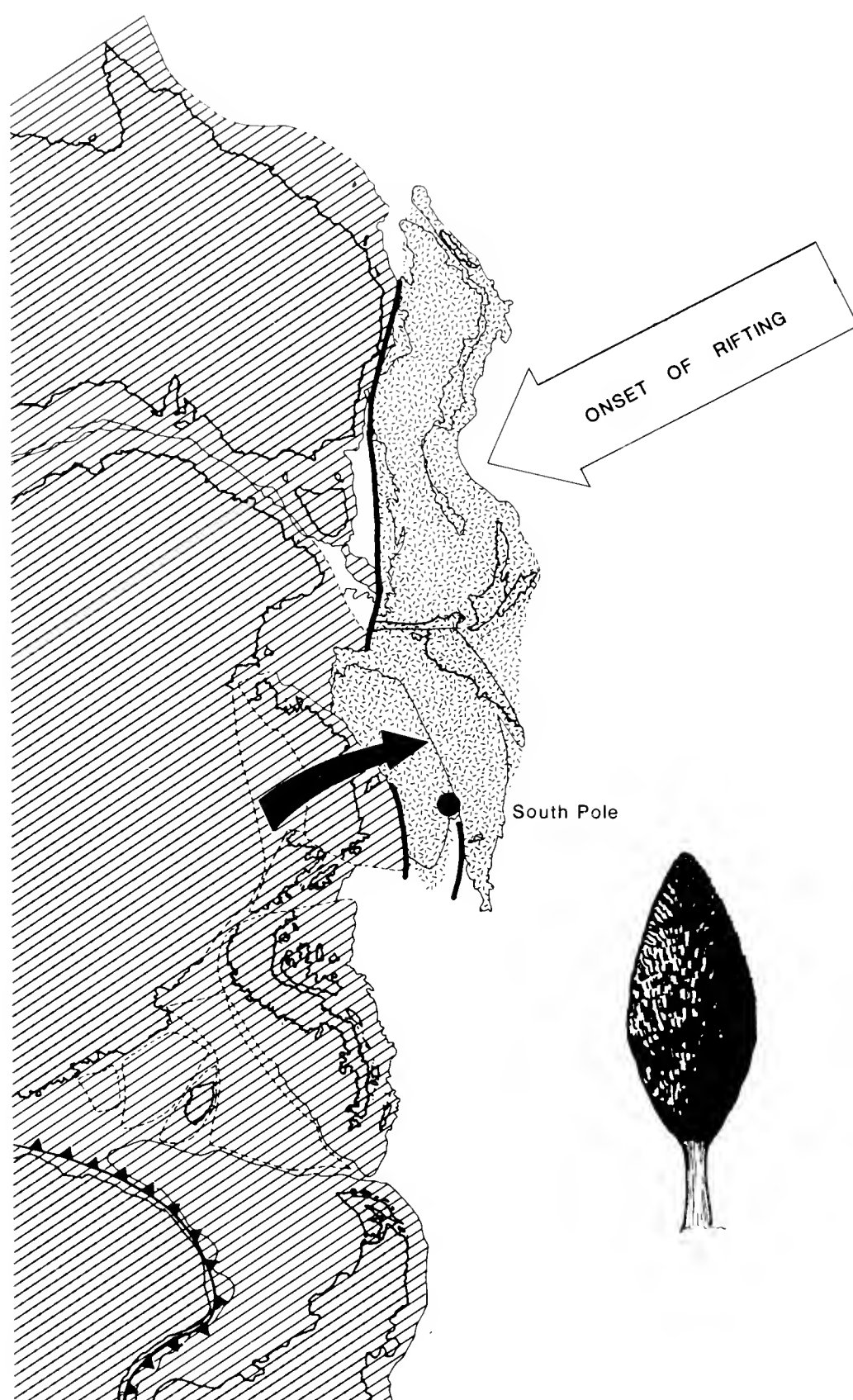


FIGURE 2 – Diagrammatic reconstruction of the southeastern margin of Gondwana in the early Cretaceous, ca. 120-110 Ma. The main uplift phases of the Rangitata Orogeny were continuing during this time. The early Cretaceous, together with the late Jurassic, constitutes the greatest extension of land in New Zealand's geological history - the development of the New Zealand microcontinent or "Greater New Zealand" (indicated by the speckled pattern). In the Aptian-Albian a rifting phase (indicated by thick lines) commenced along the west coast of New Zealand, along the western side of the Lord Howe Rise, and in the Bounty Trough. Major rifting also commenced between the African and South American plates (indicated by the toothed pattern). Ancestral angiosperms appeared at about this time and radiated throughout the Gondwana margins. Because of the disruption of land routes by the onset of rifting along the western edge of "Greater New Zealand", heralding formation of the Tasman Sea, the ancestral angiosperms may have used a land route into New Zealand via Antarctica (as indicated by the solid arrow). Ancestral ratite birds, including ancestral moas, may have also used this route (as also in the late Jurassic, Figure 1), if they were flightless at this time.

Jurassic: the New Zealand frogs, *Leiopelma*, the Tuatara *Sphenodon*, skinks and leptodactylid geckos; onychophorans (*Peripatus*); and other groups of freshwater and terrestrial invertebrates (Keast 1973, Fleming 1975, Bull & Whitaker 1975, King 1987, Worthy 1987 a, b) (Figure 1).

Although contrary opinions are held (e.g., Eskov 1987, Craw 1985, 1988), it is considered that ancestors of these modern organisms were originally widely distributed across the lands of eastern Gondwana and that establishment of land links between "Greater New Zealand" and the cratonic areas of Australia and Antarctica, then largely above the sea, facilitated their spread into New Zealand and probably New Caledonia. There is no fossil record to support such a proposal (Fleming 1975) but Gondwanan relationships are known, for example, for sphenodontian reptiles (Fraser 1986, Benton 1986), leptodactylid geckos (King 1987) and taxa related to *Leiopelma* (Estes & Reig 1973).

It is generally accepted that the Rangitata Orogeny reached its climax in the late Jurassic and early Cretaceous, (Suggate 1978). "Greater New Zealand" probably also reached its maximum size during this time. Concurrently, continuing rotation of Gondwana swung New Zealand even further northwards from its middle Jurassic position. From late Jurassic to possibly also earliest Cretaceous times, New Zealand was lying at about 55°S and was influenced by sub-tropical/warm-temperate conditions (Stevens 1980a, 1985). This period is considered to have provided the greatest (as well as probably the last) opportunity for subtropical/warm-temperate terrestrial organisms to move from southeastern Gondwana to New Zealand and New Caledonia along continuous land routes.

The early birds, newly differentiated from their ancestral reptilian stocks (Feduccia 1980, Olson 1985, Cracraft 1988), first began to occupy various ecological niches throughout the world in the late Jurassic and earliest Cretaceous. Judging from occurrences of fossil feathers, they were present in Australia at least as early as 120 Ma (Talent et al. 1966, Rich et al. 1989, Rich 1976, 1979, Rich & Baird, 1986). At this time, substantial areas of land existed in southeastern Gondwana, comprising ancestral Australia, Antarctica, New Zealand and New Caledonia. These areas probably formed one continuous landmass, with broad links to the remainder of Gondwana. Furthermore, the climate was reasonably uniform and equable, ranging from subtropical to warm-temperate. It is likely therefore that the early birds found few if any barriers, geographic or climatic, to their spread throughout eastern Gondwana in those times, providing the most propitious circumstances for at least some of the ancestral stocks of ratite birds to have become established in New Zealand (notably those of the Moa, Dinornithiformes; Cooper et al. 1990). However, this scenario assumes that the ancestral ratites were already virtually flightless and needed continuous land routes for dispersion (Fleming 1982, Stevens 1985, 1989).

EARLY CRETACEOUS

The phase during which extensive land connections existed between "Greater New Zealand" and southeastern Gondwana was brought to an end in the early Cretaceous. During this time an extensive rift system developed along the western margin of New Zealand and the western flank of the Lord Howe Rise (Figure 2). The onset of this rifting marked the beginning of movements that eventually, in the late Cretaceous, led

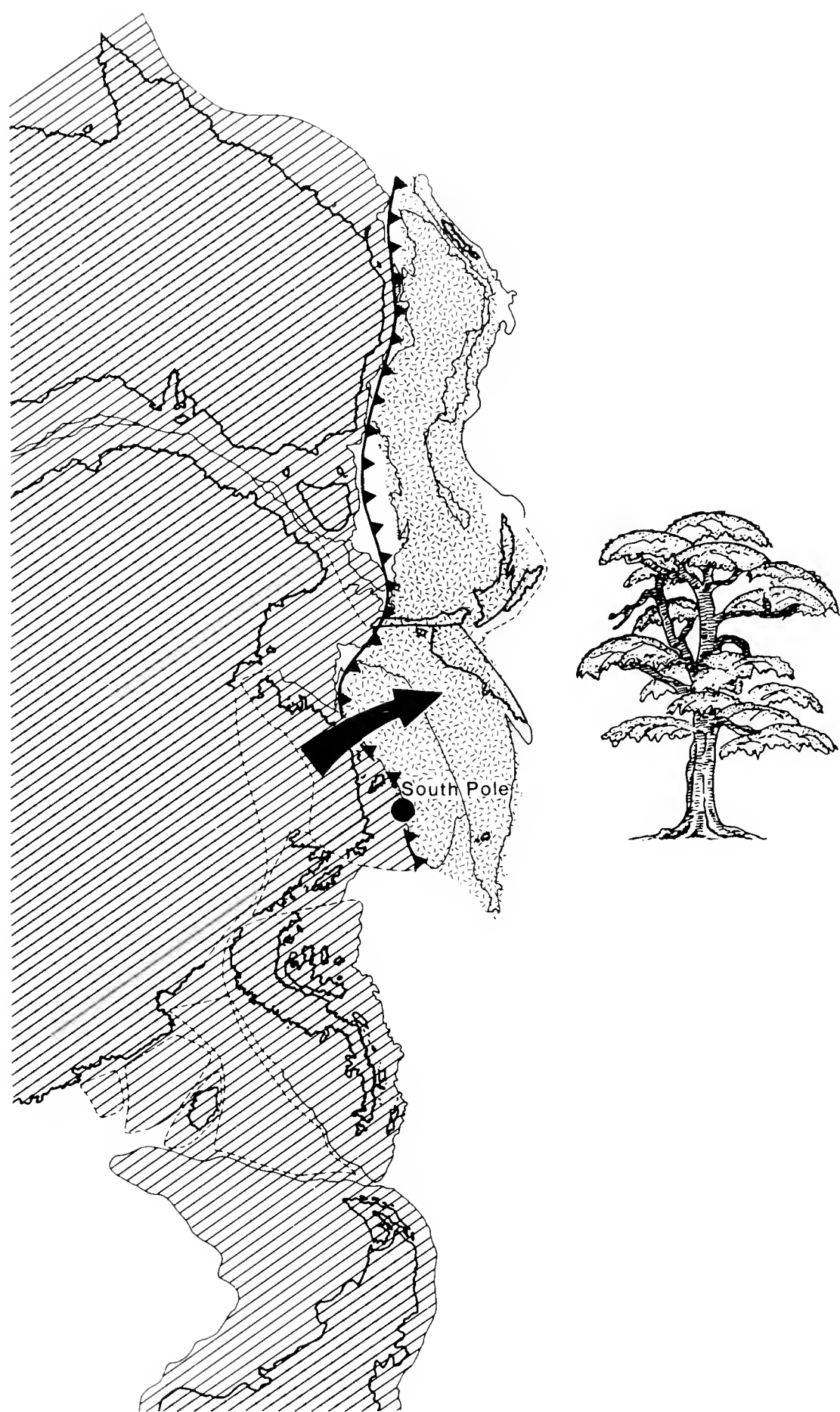


FIGURE 3 – Diagrammatic reconstruction of southeastern Gondwana in the middle Cretaceous, ca. 100-95 Ma. By this time the altitude and extent of the “Greater New Zealand” landmass uplifted by the Rangitata Orogeny (Figures 1, 2) had been markedly reduced by thermal subsidence and by erosion, both marine and terrestrial; marine transgression was commencing along the east coast of New Zealand. Active rifting, accompanied by development of finger-like marine embayments along the rift zones, was occurring along the western margin of “Greater New Zealand”, marking the sites of the future Tasman Sea and Southern Ocean (indicated by the toothed pattern). The approximate distribution of land in the New Zealand region is indicated by the speckled pattern. The ancestral stocks of Southern Beech (*Nothofagus*) and Proteaceae were radiating to southern lands at about this time, using Antarctica as a stepping stone. Entry of these stocks to New Zealand was probably via a southern route, as indicated by the solid arrow.

to development of oceanic crust in the Tasman Sea and Southern Ocean. The rifting movements began ca. 120 Ma and became particularly evident by ca. 110 Ma (Laird 1981, Whitworth et al. 1985, Spörli 1987, Tulloch & Kimbrough 1989). As the rifts progressively widened and deepened, they were invaded by long fingers of sea and pre-existing land connections became disrupted.

During the late Jurassic and early Cretaceous, continental movements began in western Gondwana that were to have major consequences in eastern Gondwana. The separation of Antarctica and India from Africa to form the Indian Ocean, and the separation of Africa from South America to form the South Atlantic Ocean, reversed the movement of eastern Gondwana that throughout the Triassic and Jurassic had been in a direction away from the South Pole (Stevens 1980b). As a result, the geographical position of southeastern Gondwana (and more particularly, that of eastern Australia and New Zealand) changed from mid-latitude in the Jurassic to high latitude in the early Cretaceous (Stevens 1980a, 1985; Rich et al. 1989). It is likely that the climatic change accompanying this rotation was equivalent to a change from sub-tropical/warm-temperate in the Jurassic to cool-/cold-temperate in the early Cretaceous (Stevens 1971, 1980a, 1985). Although ice may have been present at the North Pole during at least some of the time of the early Cretaceous (Kemper 1987), there are no indications that Cretaceous climates in New Zealand or Australia were ever colder than cold-temperate, despite New Zealand being within 5°-10° of the South Pole in the mid-Cretaceous (Oliver et al. 1979). Cool humid conditions occurred in New Zealand, South Australia and Victoria in the early Cretaceous, with a varied biota, including forest vegetation, living in markedly seasonal climates with winter temperatures dropping close to freezing (Stevens & Speden 1978, Raine et al. 1981, Rich & Rich 1988, Frakes & Francis 1988, Rich et al. 1989, Douglas 1990, Francis & Frakes 1990).

The extensive landmass of "Greater New Zealand" became exposed at this time to the effects of peneplanation and marine erosion, and of thermal subsidence of the lithosphere (Spörli & Ballance 1989). By mid-Cretaceous times, large areas of the land had been worn down to such low levels that widespread marine transgression was taking place, particularly along the eastern margin (Stevens & Suggate 1978, Stevens & Speden 1978). Erosion and diminution of the "Greater New Zealand" landmass, together with the development of active rifting zones between Australia and the western margins of New Zealand and the Lord Howe Rise, contributed to the steady deterioration of the Gondwanan land links that had been a feature of Jurassic times. However, judging from the presence of ancestral angiosperms in New Zealand from ca. 105 Ma onwards (Fleming 1975, Raine et al. 1981) (Figure 2), and of ancestral Southern Beech (*Nothofagus*) from ca. 90/85 Ma onwards (Dettmann, 1989, Dettmann et al. 1990) (Figure 3), some land links persisted, particularly towards the south, through western Antarctica to South America. The close affinities of New Zealand and South American *Nothofagus* (Poole 1987) suggest strong connections at this time for cool- or cold-temperate floras (Case, 1988, Dettmann, 1989).

Rifting and subsidence had also commenced along the south coast of Australia at about 125 Ma (Hegarty et al. 1988) or 140 Ma (Williamson et al. 1990). By about 90 Ma it gave way to an episode of slow sea-floor spreading between Australia and Antarctica (Cande & Mutter 1982, Veevers 1986, 1987, Hegarty et al. 1988, Powell et al. 1988). However, the onset of rapid seafloor spreading and substantial separation of

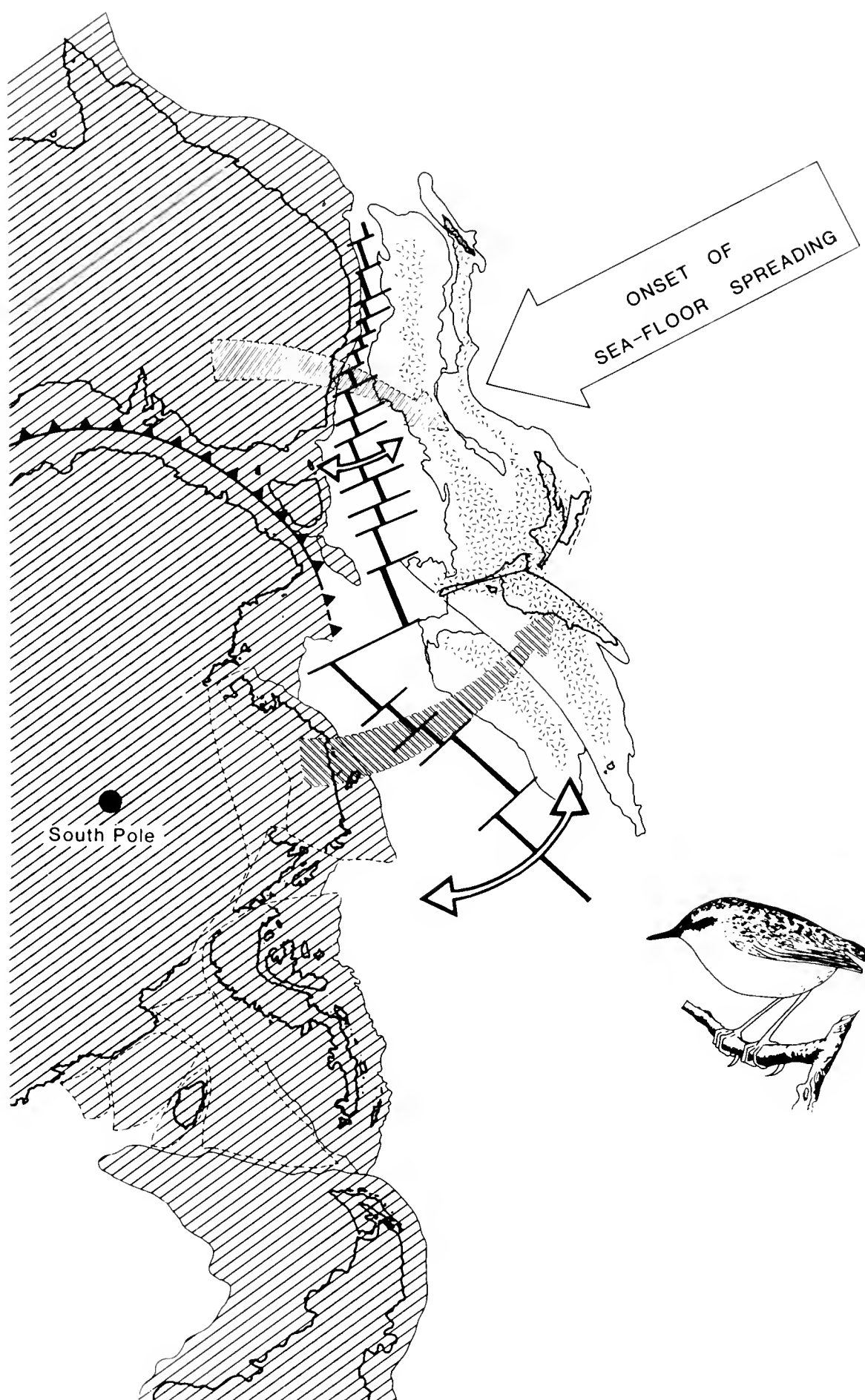


FIGURE 4 – Diagrammatic reconstruction of southeastern Gondwana in the late Cretaceous, ca. 75 Ma. Base map modified from Kamp (1986a). Rifting and slow spreading had been occurring between Australia and Antarctica since ca. 95 Ma (indicated by the toothed pattern). Active sea-floor spreading had been occurring since ca. 85 Ma in the Tasman Sea and in the sector of the Southern Ocean south of the southern edge of the Campbell Plateau (as indicated by the generalised sea-floor spreading pattern). Although land connections between the New Zealand region and the remainder of Gondwana had been broken, it was still possible for volant animals to overfly the developing oceans before they became too wide and too stormy (as indicated by the two broad striped arrows). Biochemical data suggest that ancestral stocks of the New Zealand “wrens” may have become established in New Zealand at about this time. The approximate distribution of land in the New Zealand region is indicated by the speckled pattern.

the two continents did not begin until 55 Ma (Weissel & Hayes 1972). The impact of this tectonic activity on biotic interchanges between Australia and Antarctica (and by extension, South America) between 90 and 55 Ma is difficult to evaluate because of the extremely sparse terrestrial fossil record. However, occurrences of fossil Proteaceae, *Nothofagus* and other plants (Dettmann & Thomson 1987, Pocknall & Crosbie 1988, Dettmann & Jarzen 1988, Dettmann 1989, Dettmann et al. 1990) indicate that terrestrial connections persisted across the area of rifting, probably in the region between Victoria/Tasmania and North Victoria Land, Antarctica (Veevers, 1987, Wilson et al. 1989) and that these links continued into at least the latest Cretaceous, 85-75 Ma. The distribution of fossil marsupials in the late Eocene is also indicative of the persistence of southern land connections then, presumably linking Australia, Antarctica and South America (Woodburne 1982, Woodburne & Zinsmeister 1982, 1983, 1984, Case et al. 1988, Case 1988), but not including New Zealand, where indigenous marsupials are unknown.

LATE CRETACEOUS

Expansion of the Atlantic and Indian Oceans continued at a steady rate throughout late Cretaceous time. These movements affected many sectors of southern Gondwana and had the effect of swinging New Zealand northwards away from the South Pole, so that by the late Cretaceous it lay between 65°-55°S, compared with 85°S in the early-middle Cretaceous (Stevens 1980a, b, 1985).

The same movements had also rotated West Antarctica, so that it now straddled the South Pole. Nonetheless, climatic conditions were evidently still not favourable for the accumulation of ice, as traces of late Cretaceous glaciation are unknown. On the contrary, there is abundant fossil evidence that large areas of Antarctica were probably clothed in forests (presumably of *Nothofagus* and other cool-temperate taxa; Dettmann, 1989, Dettmann et al. 1990). Therefore, as in early and mid-Cretaceous times, the climate of New Zealand, Australia and other "southern" lands was cool- or cold-temperate and had well-defined seasons (Jefferson 1982, 1983, Francis 1986, Parrish & Spicer 1988a, b, Case 1988, Pirrie & Marshall 1990).

Rifting movements that continued around the primaeval New Zealand landmass throughout early and mid-Cretaceous times culminated about 85 Ma with the establishment of open ocean in the Tasman Sea and in the Southern Ocean south of New Zealand (Figure 4). The development of open oceanic conditions brought to an end any likelihood of land connections to New Zealand and New Caledonia from Australia and the remainder of southeastern Gondwana.

As the Tasman Sea and the Southern Ocean opened, and as sea-floor spreading moved "Greater New Zealand" away from the remainder of southeastern Gondwana, its surface continued to be lowered by erosion and thermal subsidence (Kamp 1986a, b, Spörli 1987, Korsch & Wellman, 1988, Tulloch 1990). By late Cretaceous times much of it had been reduced to low relief and marine incursion was widespread.

Biochemical data indicate that the ancestral stocks of the New Zealand "wrens" (Xenicidae: Rifleman, Bush Wren, Rock Wren, Stephens Island Wren; Bull & Whitaker 1975, Fleming 1982) were established by 85 to 90 Ma (Sibley, Williams & Ahlquist

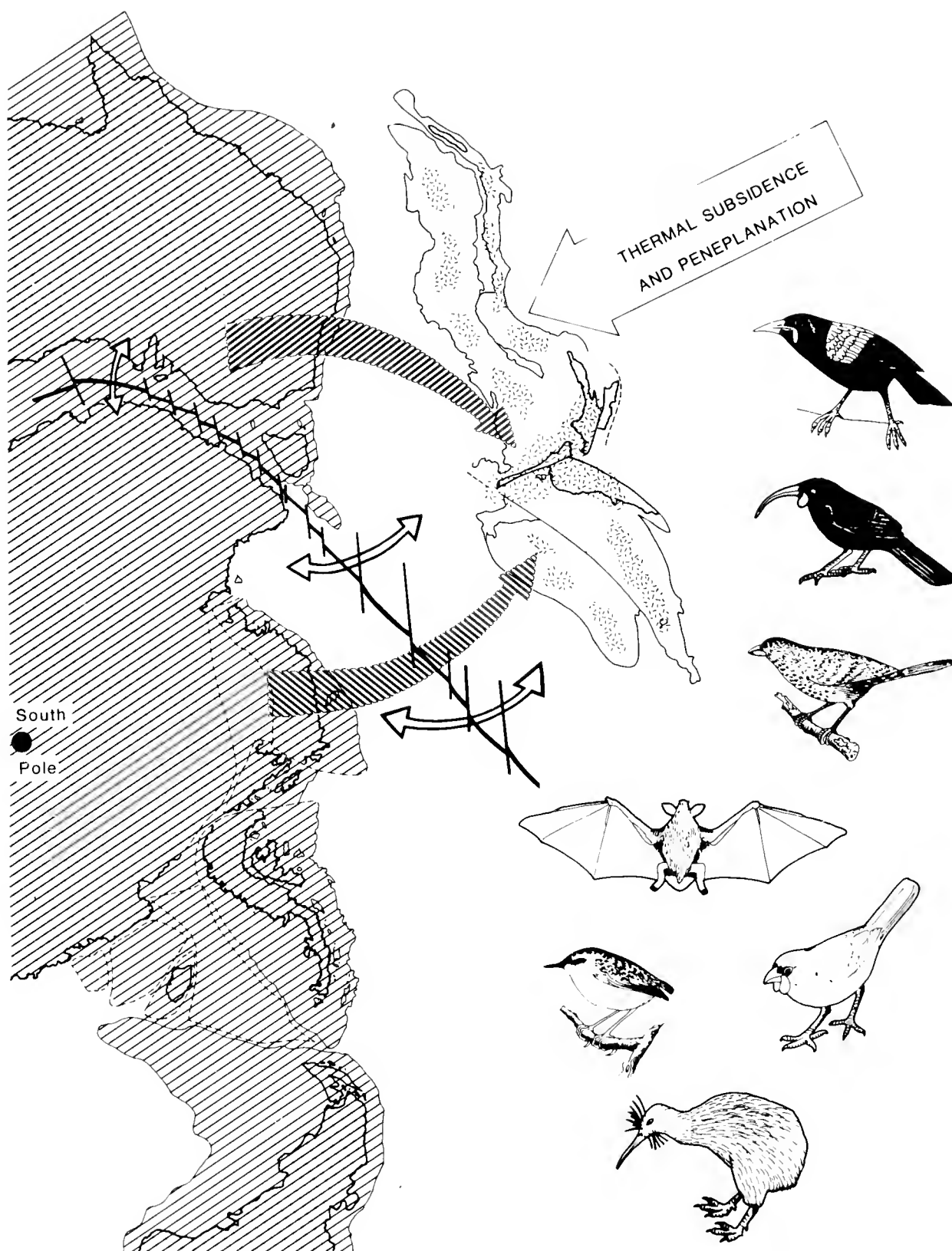


FIGURE 5 – Diagrammatic reconstruction of southeastern Gondwana in the late Paleocene, ca. 57 Ma. Base map modified from Kamp (1986a). Active sea-floor spreading had ceased in the Tasman Sea at ca. 60 Ma. Sea-floor spreading was continuing in the Southern Ocean south of the Campbell Plateau and commenced at an accelerated pace between Australia and Antarctica at ca. 55 Ma (as indicated by the generalised sea-floor spreading pattern). Although land connections between New Zealand and the remainder of Gondwana had been broken in the late Cretaceous, ca. 85 Ma, it is likely that flying animals could still cross the developing oceans (as indicated by the two broad striped arrows). Such animals may have included the ancestors of the New Zealand Short-Tailed Bat *Mystacina*, the winged ancestors of the New Zealand Kiwi *Apteryx*, and the stocks that gave rise to the endemic families of New Zealand passerine birds. The drawings along the right edge of the diagram are of representatives of families that probably became established in New Zealand during Paleocene times. From top to bottom: Saddleback *Philesturnus carunculatus*, Huia *Heteralocha acutirostris*, New Zealand Thrush *Turnagra capensis*, New Zealand Short-Tailed Bat *Mystacina tuberculata*, Kokako or Blue-Wattled Crow *Callaeas cinerea*, Rock Wren *Xenicus gilviventris*, Kiwi *Apteryx*.

1982, Sibley & Ahlquist, 1983). Although such biochemical "dating" should be regarded with caution (cf. Houde 1987, Lewin 1988a, b, Kirsch & Krajewski 1988, Erwin 1989), it nevertheless suggests that the establishment of the ancestral stocks of the New Zealand "wrens" may have occurred just before the commencement of sea floor spreading in the Tasman Sea and the Southern Ocean, and could have been co-inherited from eastern Gondwana. Given the later rifting of Australia from Antarctica, so also could the ancestral stocks of Australo-Papuan songbirds – the menceroids, meliphagoids and corvoids – have been co-inherited from Gondwana if they did not begin to diverge from one another and from Eurasian groups until about 55 or 50 Ma, as postulated by Sibley and Ahlquist (1985).

PALEOCENE

During the late Paleocene, ca. 60 Ma, the Tasman Sea had probably reached its present width (1950 km), or slightly more (as its overall width was subsequently reduced by the late Cenozoic spreading of the Lord Howe Ridge, Stock & Molnar 1982). However, sea floor spreading continued south of New Zealand, between Antarctica and the southern edge of the Campbell Plateau. From this time onwards, the ancestral Tasman Sea and Southern Ocean became effective barriers to overland routes into New Zealand, and all terrestrial colonists had to arrive by either flying or swimming/floating. Many birds did so, but no terrestrial snakes and no mammals except bats (Figure 5).

Despite its increasing isolation, the changing archipelago of New Zealand continued to receive bird colonists from nearby lands especially from Australia, where a rich and diverse avifauna was developing throughout the Cenozoic (Rich 1976).

After the ratites, which may have come by land (see above), the next bird colonists known to have arrived were the endemic families of New Zealand passerines - the New Zealand "wrens", wattlebirds and "thrushes" (Xenicidae, Callaeatidae and Turnagridae) of uncertain relationships, but some showing "Gondwana" affinities with the ovenbirds and antbirds of South America, the lyrebirds of Australia and the pittas of the Old World tropics (Bull & Whitaker 1975, Fleming 1977b, 1982). The ancestral stocks of these endemic bird families may have arrived in the Paleocene, before the seas then opening around New Zealand became too wide and stormy. However, as mentioned earlier in this paper biochemical data point to the possibility that the ancestral stocks of at least one endemic bird family - the New Zealand "wrens" - may have radiated to New Zealand in late Cretaceous times (95-90 Ma, according to Sibley & Ahlquist 1983).

At the same time as the ancestral stocks of the New Zealand endemic passerines were traversing the seas then opening up around New Zealand, the ancestors of the New Zealand Short-Tailed Bat *Mystacina* may have made a similar journey. Biochemical studies of *Mystacina* have demonstrated that it has close phylogenetic affinities with Central and South American phyllostomid bats and have suggested (using the assumption that bats originated in the Paleocene) that the lineages separated about 35 Ma (Daniel & Baker 1986, Pierson et al. 1982, 1986). It is therefore likely that the ancestral stocks of *Mystacina* followed a route from South America via Antarctica, and although as noted earlier such biochemical "dates" should be used with caution, radiation may have occurred sometime in the early Paleogene.

Judging from deep sea drilling (e.g. Barker et al. 1987, Kerr, 1987) and palynological studies (e.g. Truswell 1984, Dettmann et al. 1990), large parts of Antarctica were forested during the Paleogene, until at least the early Oligocene. These forested areas may have offered a trans-Antarctic connection with South America for ancestral *Mystacina* which, on encountering the steadily widening oceanic gaps then present around New Zealand, flew across them to colonise the "Greater New Zealand" land-mass. Such a passage may have been via the Campbell Plateau, areas of which were emergent at this time (Figure 5). An alternative route may have involved radiation across Antarctica, thence into Australia and then via a route into New Zealand by means of island-hopping southwards along the Lord Howe Rise. The possible use of this alternative route is suggested by the presence on *Mystacina* of a tick normally parasitic on Australian bats (Daniel 1979).

The volant immigrants that came to New Zealand in early Paleogene times by flying across the newly created surrounding oceans may have also included at least some of the flying ancestors of the ratites, particularly those of the Kiwi (*Apteryx*), if the views of Houde (1986), Howgate (1986) and the biochemical data of Sibley and Ahlquist (1987) and Cooper et al. (1990) are accepted.

The opening-up of ocean between New Zealand and the southeastern margin of Gondwana had the effect of moving New Zealand and New Caledonia northwards away from the South Pole, so that in the Paleocene they were in latitudes of 50°-45°S compared with 65°-55°S in the late Cretaceous (Stevens 1985).

The effects of this northwards movement are evident in the New Zealand marine faunas, as indicated by increasing influxes of warm-water Malayo-Pacific molluscan taxa beginning in late Paleocene times (Fleming 1967b, 1975, Beu & Maxwell 1968, Beu et al. 1990, Hornibrook 1978).

EOCENE

Sea-floor spreading finished activity in the Tasman Sea in the late Paleocene, ca. 60 Ma. Subsequently, sea-floor spreading became focussed in the Southern Ocean south of New Zealand and Australia. Although rifting between Australia and Antarctica had been occurring since the late Cretaceous, ca. 95 Ma (Cande & Mutter 1982; Veevers 1986, 1987), active sea-floor spreading did not commence until early Eocene, ca. 55 Ma. After this time, Australia and Antarctica moved apart, although contact via the South Tasman Rise (extending southwards from Tasmania) continued until ca. 35 Ma (Kennett et al. 1975). As Antarctica moved southwards, Australia and New Zealand moved northwards. New Zealand's geographic position changed from 50°-45°S in the Paleocene to 45°-40°S latitude in the late Eocene (Stevens 1985).

The gradual build-up of ice on Antarctica, commencing on East Antarctica in the earliest Oligocene (or earlier in highland valleys) and on West Antarctica in the late Miocene (Barker et al. 1987; Barron et al. 1988), combined with the opening-up of surrounding seaways put an end to Antarctica's role as a stepping stone for southern migrants. At the same time, these developments led to the establishment of Circum-Antarctic wind and ocean current systems (Kennett et al. 1975, Barker & Burrell 1977). As these systems reached their optimum development (typified by the

West Wind Drift), increasing numbers of plants and animals adapted to dispersal became distributed around the southern lands (the "Neoaustral" elements of Fleming 1975), including shore and pelagic birds such as penguins (Figure 6).

TRANS-TASMAN CENOZOIC LINKS

Although Australia has contributed to New Zealand's flora and fauna throughout most epochs of geological history, trans-Tasman migration was greatly strengthened by the advent of the West Wind Drift, following the separation of Australia and Antarctica. Consequently, from Miocene times onwards there was a marked increase in the



FIGURE 6 – By late Eocene times, ca. 42 Ma, widening oceanic gaps had made the possibility of shallow-water marine links between the southern lands very remote. Southern seas were beginning to be stirred by marine current systems that were the forerunners of the modern Circum-Antarctic Current, although full development of an integrated system was delayed until the South Tasman Rise had cleared the east Antarctic shelf at ca. 34 Ma (Kennett et al. 1975) and the Drake Passage had opened up between South America and the Antarctic Peninsula at ca. 29 Ma (Barker & Burrell 1977). Nonetheless, sufficient migration opportunities were available for ancestral penguins to achieve a broad southern distribution and many other marine groups with good dispersal capabilities, either as adults or juveniles achieved similar distributions by utilising the developing Circum-Antarctic marine currents.

immigration into New Zealand of Australian plants and animals, both marine and terrestrial. A notable feature of the late Cenozoic was the arrival of many land birds of Australian origin, via storm-generated westerly gales. As a result, the modern New Zealand bird fauna has a strong Australian aspect, generated by multiple colonisation. The Takahe, for example, is derived from an old (Miocene-Pliocene?) immigration of *Porphyrio* stock and has diverged considerably, whereas the Pukeko, which is indistinguishable from Australian forms, is evidently from a very recent (Holocene?) migration (Fleming 1982).

A feature of those birds that became isolated in New Zealand were adaptations to flightlessness and gigantism. The New Zealand environment, without flesh-eating predators, tended to encourage flightlessness and also the development of ground-nesting habits. Loss of flight in turn paved the way to giantism, and as the birds became larger other changes occurred: the feathers grew heavier and sparser, the legs stouter and shorter, and the brain became relatively small in relation to the beak, jaws, and cheek muscles. This was a response to the adoption of a grazing habit. The Takahe, Kakapo, and Extinct Goose (*Cnemiornis*) are examples of late Cenozoic land bird migrants that became large and flightless (Fleming 1982).

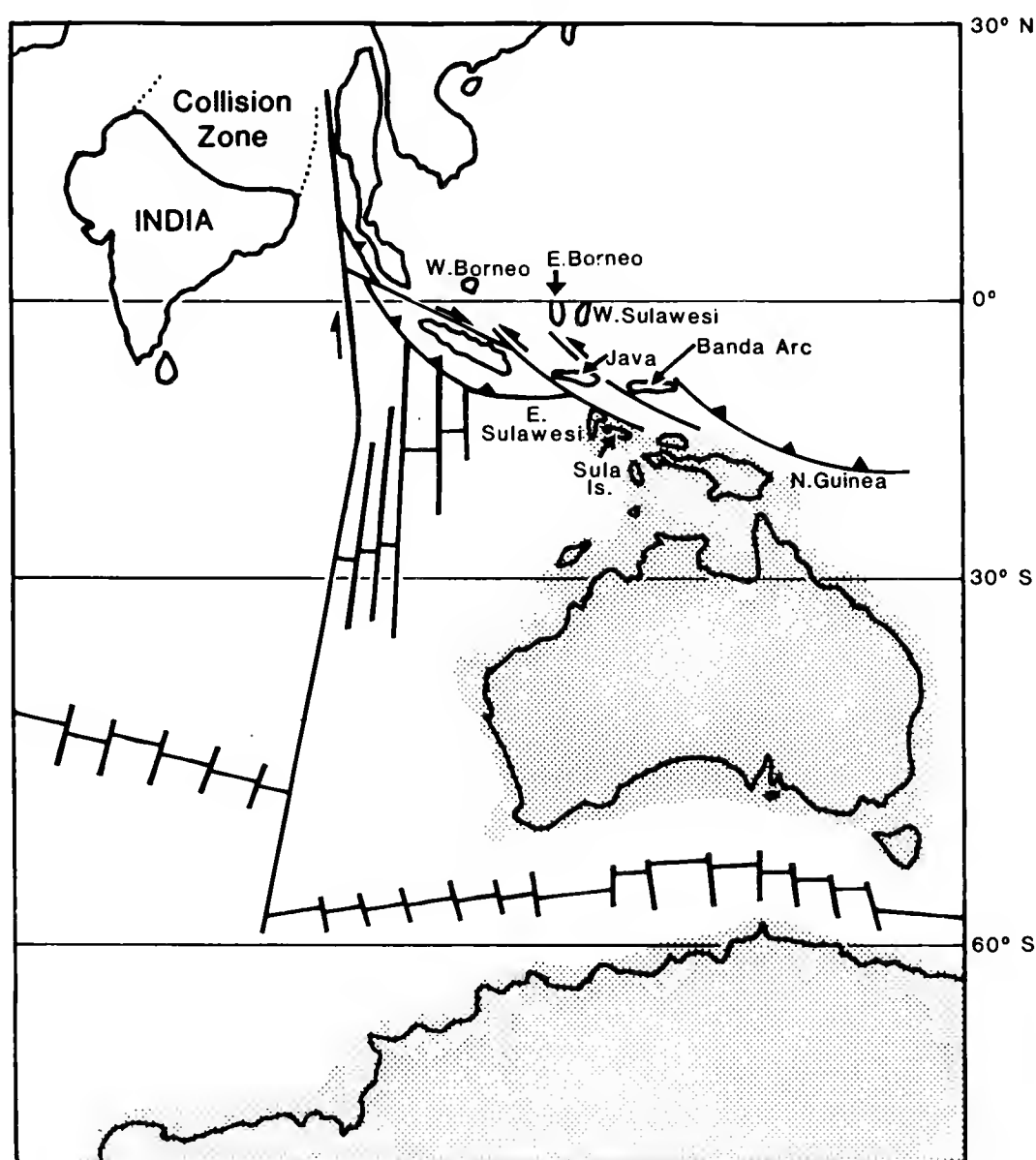


FIGURE 7 – Reconstruction of Australia and South-east Asia at ca. 40 Ma (late Eocene). At about this time a major arc-continent collision commenced just north of New Guinea and the new land areas that resulted provided opportunities for the interchange of terrestrial floras and faunas between Australia and southeast Asia. India began to collide with southern Tibet at about 44 Ma. Figures 7 & 8 are based on Audley-Charles et al. (1988). The modern continental outlines are for reference only.

SOUTH-EAST ASIAN LINKS

Although there had been links between Australia and South-east Asia extending back into Mesozoic time, they were largely ephemeral, via volcanic islands that appeared and disappeared in concert with waxing and waning volcanic activity (Cox 1990, Audley-Charles et al. 1988, Audley-Charles 1988). Substantial links did not begin to appear until the early Neogene (Figure 7). As Australia moved northwards, the fringes of island arcs, depositional troughs and allochthonous terranes along its northern boundary (that were later to give rise to Papua New Guinea and adjacent islands) began to interact with the southern edge of the Indonesian arc, as Indonesia and southeast Asia moved southwards in response to the opening and continued expansion of the South China Sea (Audley-Charles 1987, 1988, Audley-Charles et al. 1988, Hutchison, 1989, Pigram & Davies 1987, Truswell et al. 1987). Such interaction soon developed into a major collisional situation that progressively deformed and coalesced the former volcanic arcs, terranes and the contents of depositional troughs.

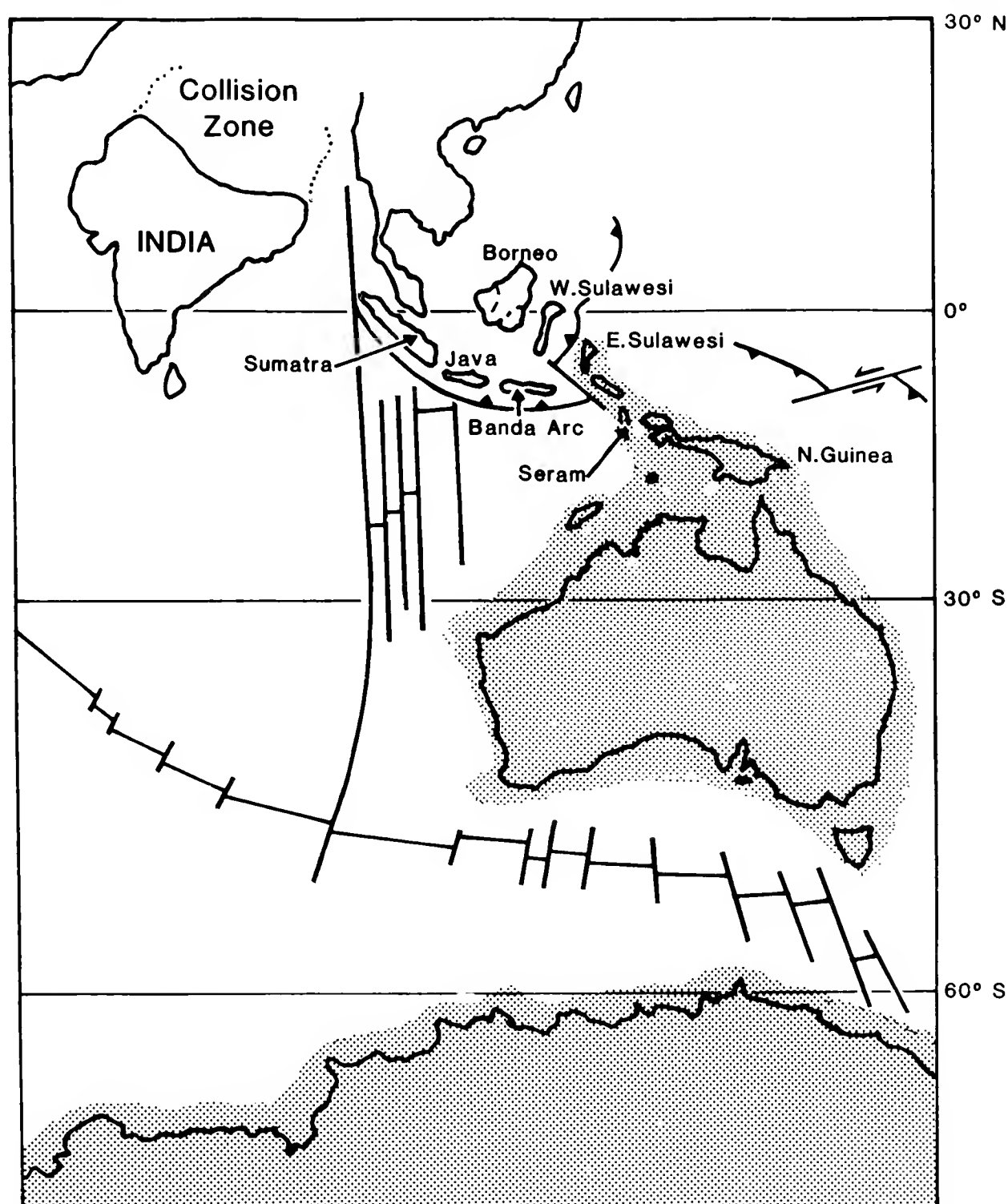


FIGURE 8 – Reconstruction of Australia and Southeast Asia at ca. 30 Ma (late Oligocene). The continuing northward movement of Australia has reinforced the extent of the South-east Asian connections seen in Figure 7.

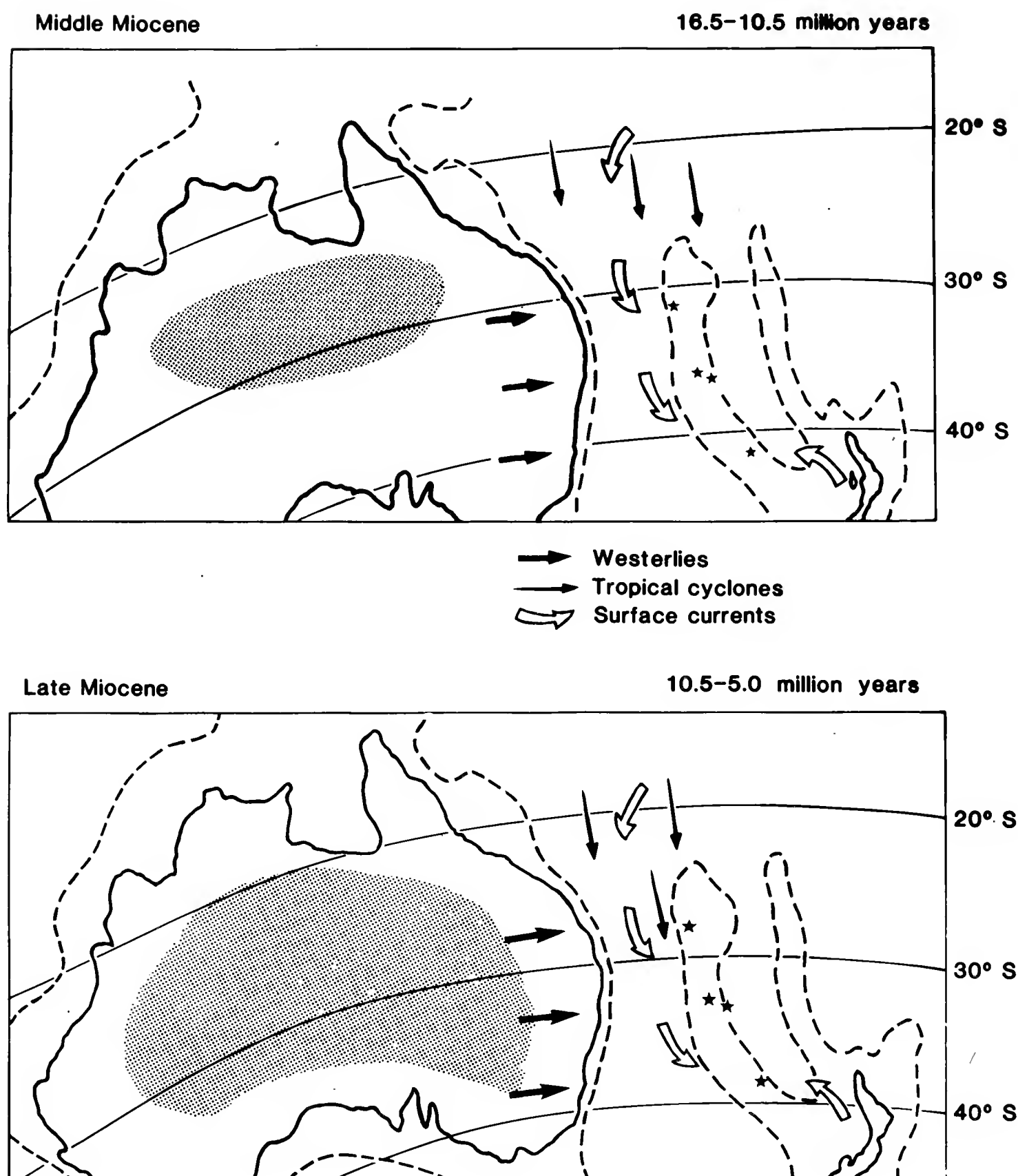


FIGURE 9 – As Australia moved northwards the areas affected by aridity progressively increased, as indicated in this diagram by the dot pattern. The growth of aridity is recorded by the changing composition of clay minerals in sediments laid down on the Lord Howe Rise, the clay minerals changing in response to increase in the amount of wind-blown material derived from the growing areas of desert and semi-desert. The drilling sites along the Lord Howe Rise that provided the clay mineral information and dating are indicated by stars. Modified from Stein and Robert (1986, Figure 12).

The first indications of earth movements related to contact between Papua New Guinea and the Indonesian/Southeast Asian arc appeared about 40 Ma ago (Figure 7). Then, as a response to major changes in the direction of motion in the Pacific Plate (Fortuin et al. 1988, Hall 1987, Kroenke 1984, Audley-Charles 1987, Audley-Charles et al. 1988), earth movements continued from the late Eocene to middle

Miocene (Figure 8). As a consequence, a large block of new land was raised, roughly aligned along the site of modern Papua New Guinea, to form a northern edge to the Australian continent (Whitmore 1982). Later, in the late Miocene and Pliocene, a seaway developed between Papua New Guinea and Australia, but intermittent land connections were renewed during the glacio-eustatic low sea levels of the Plio-Pleistocene. Such connections remained through to the Last Glacial, when a broad plainland existed across large areas of the sites of the modern Arafura Sea and Torres Strait (e.g. Walker 1972, Heatwole, 1987). This land connection was finally broken by the Flandrian sea level rise beginning about 10,000 years ago.

THE DESERTIFICATION OF AUSTRALIA

The northwards movement of Australia in the late Cenozoic brought it into progressively drier climatic belts, with the result that the widespread humid vegetation of the early Cenozoic gave way to desert and semi-desert between the late Oligocene/early Miocene (27-24 Ma) and middle Miocene (15 Ma) (Chamley 1986, Kemp 1978, 1981, Truswell & Harris 1982, Truswell 1990, Bowler 1976) (Figure 9). In northern and central Australia levels of aridity progressively built up to reach maxima coinciding with major cooling events in the late Miocene (5 Ma) and late Pliocene (2.5 Ma) (Locker & Martini 1986, 1989, Stein & Robert 1986); and concurrently, climates in southern Australia underwent alternating humid and semi-arid cycles (Stein & Robert 1986, Kennett & von der Borch 1986). Consequently, as large parts of northern and central Australia progressively became dominated by desert and semi-desert, the humid fauna, notably the birds, took refuge in the rain forest areas that still persisted in pockets along the east coast (Schodde 1982).

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THE ORIGIN AND RADIATION OF AUSTRALASIAN BIRDS: PERSPECTIVES FROM THE FOSSIL RECORD

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ABSTRACT. The avian fossil record of Australasia is patchy in its temporal and faunistic representation, much of it restricted to the Pleistocene. Australia has by far the longest avian record, dating from the Cretaceous, still richest for the Quaternary but growing for the Tertiary. The record is too scanty and uncoordinated between major regional landmasses to trace connections between them, and it says more on the radiations, early diversity and previous distribution than on origins. Few groups have a rich enough record for useful phylogenetic studies. Nonetheless the record is starting to provide crucial documentation for a broader picture of Australasian bird evolution and an interpretation of climatic and environmental changes, and should increasingly provide tests of theories on origins, colonisation routes and divergence times and document changing distributions and early faunal connections.

Keywords: Fossil record, Australia, New Zealand, New Caledonia, New Guinea, Australasia, evolution, radiation, colonisation, Tertiary, Quaternary.

INTRODUCTION

This summary is fortunate in following several recent reviews of the avian fossil record in Australasia: New Zealand (Fordyce 1982), New Guinea (Rich & van Tets 1982), New Caledonia (Balouet & Olson 1989) and Australia (Rich & van Tets 1982, Rich & Baird 1986, Baird in press, Rich in press). It presents an overview of the region and updates some aspects raised by these authors, but cannot attempt their level of detail. References are generally restricted to studies that have appeared since these reviews. For more thorough discussions and references not cited in the text, consult these reviews and Olson (1985).

FOSSIL RECORD OF MAJOR REGIONAL LANDMASSES (Figure 1)

Australasia has a patchy record, both in temporal and faunistic representation and in palaeontological research. Although richer and longer for Australia than for New Zealand, New Caledonia and New Guinea, the record is poor compared with those of Europe and North America.

New Zealand

The early fossil record of birds in New Zealand is scanty. Most Palaeogene taxa are Sphenisciformes, with scattered seabirds and some as of yet unstudied material. Although the record extends from at least the Palaeocene, other than for penguins it is sparse and uninformative.

Moas are first recorded from Pliocene deposits, but reached their greatest richness in the Pleistocene, when they became a dominant component of the record until the Recent; two families, six genera and 11 species are currently recognised (Cracraft 1976, Worthy 1988 and references therein).

Material from the Late Pleistocene forms the vast majority of the known record, much referable to living taxa. Genera no longer present in New Zealand include a range of anseriforms, some extinct and others living but now extralimital; several large raptors; a large owlet-nightjar; the extinct Apterornithidae, gruiforms of uncertain affinities; and a greater diversity and distribution of the New Zealand wrens (Acanthisittidae) (Fordyce 1982, Millener 1988).

New Guinea

The only two sites providing avian fossils, one Pliocene, one Pleistocene, have yielded cassowaries *Casuarius* (Rich & van Tets 1982, Rich et al. 1988).

New Caledonia

Published deposits are Late Quaternary, mostly Late Holocene, and indicate a greater diversity of taxa than that on the island today. The best known is the large flightless *Sylviornis*, originally thought to be a ratite, and later considered to be galliform (Poplin

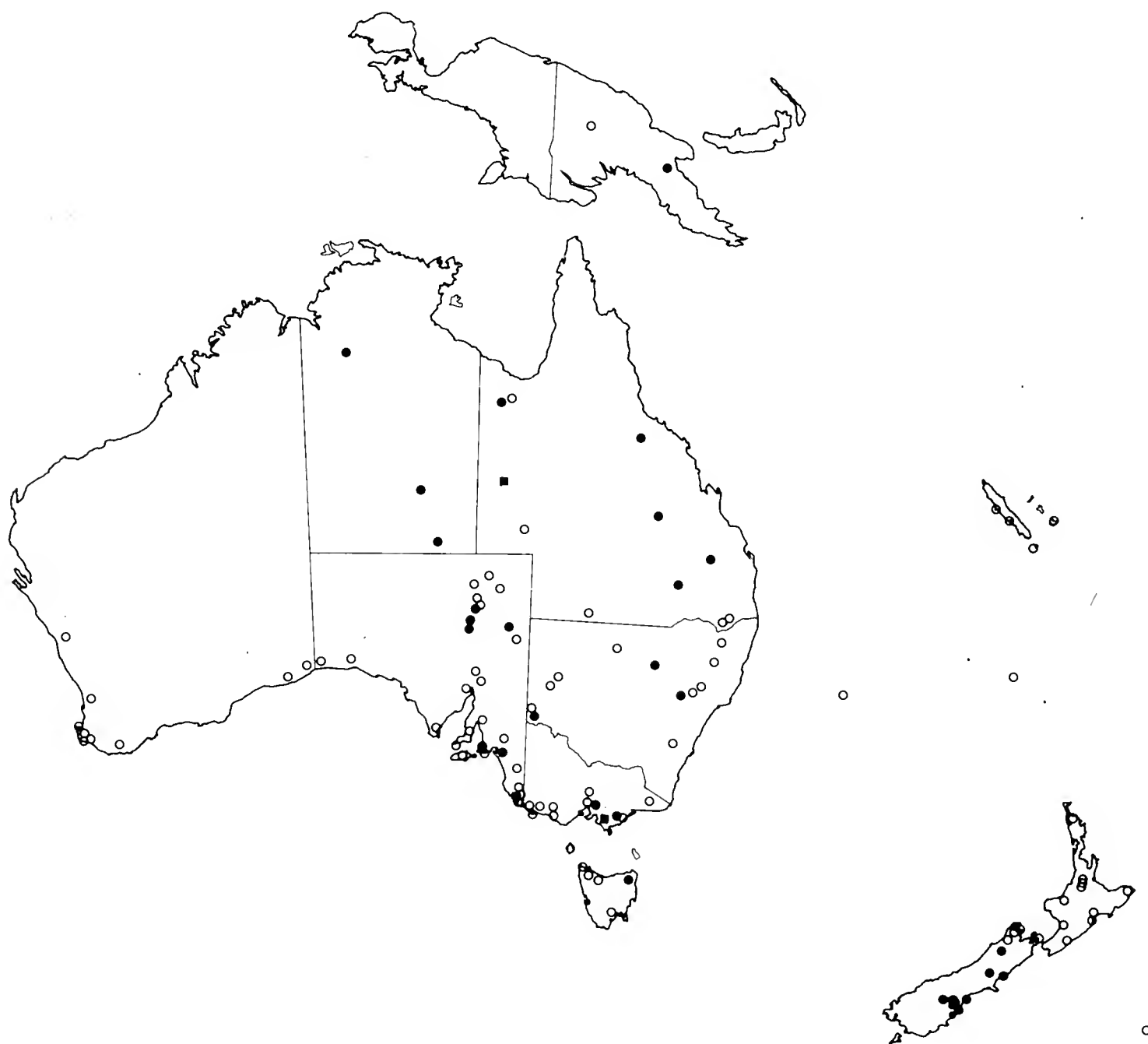


FIGURE 1 – Localities producing fossils birds in Australasia. Black triangles, Mesozoic; black circles, Tertiary; white circles, Quaternary. Late Pleistocene and Holocene sites represented only by moas (Dinornithiformes) have been omitted. Adapted primarily from Rich and Baird (1986, Figures 1, 2), Fordyce (1982) and Balouet and Olson (1989, Figure 1).

& Mourer-Chauviré 1985, Balouet & Olson 1989), possibly a giant megapode. Balouet & Olson (1989) reported on 32 nonpasserine species, including 11 now extinct. Among the latter were representatives of extant genera previously unknown from New Caledonia, but currently distributed elsewhere, e.g., northern Melanesian islands, smaller islands off New Zealand, and Asia and neighbouring islands. Information on the passerines has not yet been published.

Australia

Australia has by far the longest avian fossil record in Australasia, dating from the Cretaceous. The Quaternary is richest, both numerically and taxonomically, but the Tertiary record is growing. Cretaceous records consist of a enantiornithine tibiotarsus from Queensland (Molnar 1986) and five small indeterminate feather impressions from Victoria. Avian remains from the extensive gap between 100-22 myBP, when birds were differentiating and southern land masses were connected, lack taxonomic diversity, are restricted geographically, or are yet unstudied. The Eocene record comprises penguins, which continue into the Oligocene as virtually the only birds of this age. Of the few other remains until the Late Oligocene, the most significant are recent finds from Murgon, southeastern Queensland (54 myBP) that await study.

There are only two major intervals with rich, diverse avian records. The first, starting in the Late Oligocene and continuing through the Neogene, is represented in the present Great Artesian Basin (Lake Eyre and Lake Tarkarooloo sub-basins) of central Australia and in northern Australia (Figure 1); western Australian sites have not yet been exploited.

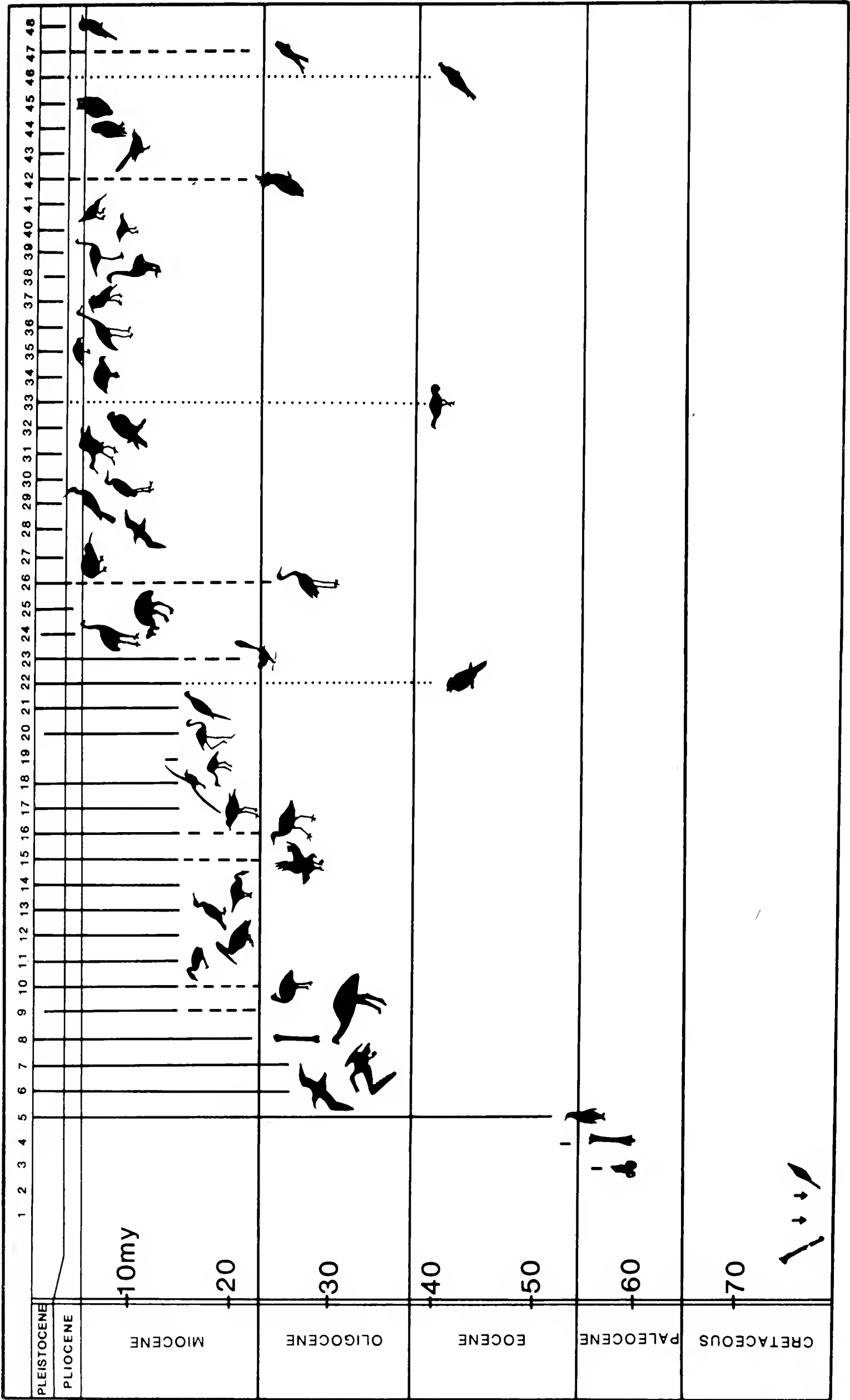
Diverse groups of non-marine birds were present in Australia at least as far back as the mid-Tertiary. Because the deposits are fluvial/lacustrine accumulations, the taxa dominating at almost every site are waterbirds, augmented by some terrestrial, often flightless, forms and scattered volant non-aquatic forms. Smaller birds are represented in central Australian sites, but by and large, most preserved pre-Quaternary taxa were medium to large, leading Rich & Baird (1986) to comment "no single locality in Australia in the pre-Pleistocene . . . has produced a diverse avian microfauna."

Important recent finds include the Riversleigh deposits, northwestern Queensland, currently under study by W. Boles. This area is significant because of its array of both water- and forest-dwelling forms, including numerous passerines. The earliest deposits are considered ?Late Oligocene-Early Miocene, with sites known through the Pleistocene; most are Miocene (Archer et al. 1989).

The second important fossil-bearing interval consists mainly of Late Quaternary cave and aeolian-fluvial deposits, principally across the southern Australia. The Dromornithidae (*Genyornis*), giant megapodes *Progyura* and some living families now absent from Australia (flamingoes, Phoenicopteridae; Rich & van Tets 1982) persisted until the Pleistocene. Most remains are referable to modern genera or species, whose distributions were often more extensive than at present (e.g. Tasmanian Native-hen *Gallinula mortierii*; Baird 1986).

Rich & van Tets (1982: Figure 27) exhibited the known fossil record of Australian bird families. Figure 2 shows the extensions in the temporal ranges revealed since, most attributable to finds from Riversleigh.

FIGURE 2 – See caption opposite page.



Australia's Tertiary fossil record suffers from several deficiencies. The different taphonomic forces of the Quaternary have yielded more complete remains than the usually incomplete and disassociated Tertiary material. Differences in the types of preservation and accumulating factors between pre-Quaternary and Quaternary deposits often renders them incomparable. Another drawback of the pre-Quaternary record is the paucity of radiometrically dated sites. Most dates have been assigned through tenuous sequences correlating remains between a series of sites (Rich & Baird 1986).

TAXONOMIC SCOPE OF THE FOSSIL RECORD

The fossil record reveals more on the radiations, early diversity and previous distributions than it does on the origins of different groups of Australasian birds. Rich & van Tets (1982) considered Australian Neogene taxa to be a mixture of archaic and modern forms: (a) possible remnant Palaeogene radiations, (b) representatives of families extant elsewhere, (c) representatives of families now extinct, and (d) more primitive members of extant families in Australia. The records of these groups vary considerably, and most suffer from deficiencies that restrict their interpretation.

Too many families that are abundant in the modern avifauna have a scanty or non-existent fossil record, or one that is restricted to the Pleistocene. Therefore, little can be said about their early history in Australasia (e.g., Columbiformes, Psittaciformes). Other groups have a relatively good Tertiary representation but have yet to receive the necessary attention. In contrast to the well documented anseriforms of Australia's and New Zealand's Quaternary, those of the Tertiary still require extensive study, as do passerines from as far back as the Late Oligocene.

FIGURE 2 – Geologic ranges of major groups of Australasian birds, modified from Rich and van Tets (1982, Figure 27) for Australia, to which have been added data from New Zealand and New Caledonia. Dashed lines are chronological extensions based on material from Riversleigh, Queensland; dotted lines are extensions of 'Australasian' groups from the Phosphorites du Quercy (Mourer-Chauviré 1982, 1989). 1, enanthiornithine birds; 2, Koonwarra feathers; 3, unidentified bones, Murgon, Queensland, Australia; 4, unidentified bones, Waimakariri River, New Zealand (Fordyce 1982); 5, Sphenisciformes (penguins); 6, Diomedidae (albatrosses); 7, Pelagornithidae (=Odontopterygidae *auct*) (bony-toothed birds); 8, unidentified bones, Waihao River, New Zealand (Fordyce 1982); 9, Dromornithidae (mihirungs); 10, Dromaiinae (emus); 11, Podicipedidae (grebes); 12, Pelecanidae (pelicans); 13, Phalacrocoracidae (cormorants); 14, Anatidae (waterfowl); 15, Accipitridae (hawks, eagles); 16, Rallidae (rails); 17, Burhinidae (stonecurlews); 18, Laridae (gulls); 19, Palaelodidae (*Palaelodus*); 20, Phoenicopteridae (flamingoes); 21, Columbidae (pigeons); 22, Aegothelidae (owlet-nightjars); 23, Passeriformes (songbirds); 24, Dinornithiformes (moas); 25, Casuariinae (cassowaries); 26, Ciconiidae (storks); 27, Apterygiidae (kiwis); 28, Procellariiformes (petrels, shearwaters); 29, Anhingidae (darters); 30, Ardeidae (herons); 31, Threskiornithidae (spoonbills, ibis); 32, Falconidae (falcons); 33, Megapodiidae (megapodes); 34, Phasianidae (quail); 35, Turnicidae (button-quail); 36, Gruidae (cranes); 37, Rhynochetidae (kagus); 38, Apterornithidae (*Apterornis*); 39, Otidae (bustards); 40, Pedionomidae (plains wanderers); 41, Charadriiformes (waders); 42, Psittaciformes (parrots, cockatoos); 43, Cuculidae (cuckoos); 44, Tytonidae (barn owls); 45, Strigidae (typical owls); 46, Podargidae (frogmouths); 47, Apodidae (swifts); 48, Alcedinidae (kingfishers).

Some groups have temporally restricted records that are well studied but not extensive enough to allow useful extrapolation beyond those particular fossils, e.g., the pelicans of Australia, Quaternary rails and waterfowl of Australia and New Zealand, the megapodes *Progura* of Australia, and *Sylviornis* of New Caledonia.

A few families have diverse, well-documented records, which provide information on radiation and diversity of the groups — but no useful clues to their origins. The moas (Dinornithidae, Emeidae) have no doubt the most detailed record of any Australasian group, but it is so restricted in time that it offers little on their early history. Similar comments apply to the Dromornithidae, which have a longer but less representative record, and the Sphenisciformes, which have one of the longest fossil records of any extant group.

Of considerable interest are groups that demonstrate early avifaunal connection with other continents: either their earliest record is not Australasian or similarly-aged remains are known from both areas. Prominent examples of the latter are the flamingoes, known in central Australia from the mid-Tertiary until the Pleistocene, a record paralleled in Africa and the Northern Hemisphere, and the now extinct Palaelodidae (Baird & Rich in press). Three groups considered among the most characteristic of the Australasian region (megapodes, Megapodiidae; frogmouths, Podargidae; and owl-nightjar, Aegothelidae) have their earliest records in the Eo-Oligocene deposits of France and Germany (Mourer-Chauviré 1982, 1989, Peters this symposium); only the last has pre-Quaternary remains from Australasia (Figure 2). Because Australasia has no Palaeo-Eocene record, the first real occurrence of these groups is open to question and the significance of these European records cannot be evaluated.

ORIGINS AND EXTINCTIONS

The pre-continental drift concept of Australasian bird origins derived them from five major 'waves' of northern emigrants: the earliest colonisations giving rise to the most differentiated taxa, through to the most recent, which are only subspecifically distinct from otherwise Old World taxa (Mayr 1944). Acceptance of continental drift and plate tectonics turned biogeographers efforts to identifying which modern Australasian taxa may have had southern origins (e.g. Cracraft 1972, Rich 1975, Schodde 1982). Evidence for a group's Gondwanan origins included its degree of endemism, distribution of its closest relatives, and richness and diversity on each continent. Biochemical techniques identified several higher taxa that may have had their origins in Gondwanaland (reviewed by Christidis, this symposium).

Such compilations have been generally based on nonpalaeontological criteria. Olson (1989) attempted to identify such groups based at least in part on the fossil history. He suggested that many groups characteristic of the modern Australasian avifauna may be relictual, as were possibly most avian groups with principally southern distributions, but nominated five groups that could have had austral beginnings: grebes, ducks, pigeons, parrots and passerines.

The Australasian fossil record is too inadequate to be useful for the first four groups. Its passerine record, however, is of comparable age with the oldest known from the Northern Hemisphere (Mourer-Chauviré et al. 1989). One Australian mid-Miocene

specimen cannot be separated generically from the logrunners *Orthonyx* (Boles, unpub.), among Australasia's most distinctive living endemic songbird genera. The fossil record does not deny, even if it does not confirm, the antiquity of the Australasian land bird fauna and the older endemic radiation in songbirds postulated by current molecular studies. However, it can in some instances test suggested divergence times emerging from these studies.

The Australasian avifauna may have had multiple origins, but the portions attributable to dispersal and to vicariance are unclear. To make more significant contributions, the fossil record needs additional material from crucial times, supported by a better understanding of avian relationships (Rich & van Tets 1982).

As more remains are found and identified, and earlier misidentifications corrected (e.g. van Tets & Rich 1990), the extent of Pleistocene extinctions can be more accurately assessed. Habitat deterioration starting in the Miocene and climatic oscillations of the Pleistocene caused loss of extensive inland lakes in Australia. Waterbirds, particularly flamingoes, and possibly other families, presumably died out as a result. Older bird groups that radiated in the Palaeogene were already showing a post-Tertiary reduction in diversity and may have also been terminally affected (e.g. Dromornithidae, Rich & van Tets 1982). Gigantism was prominent during the late Tertiary and Quaternary and large taxa, such as moas, *Genyornis*, *Progunya* and *Sylviornis*, appeared foremost among the extinctions. Perhaps this is over emphasized because of the preferential preservation and relative ease of finding large bones and a preference of paleo-ornithologists for studying them. The growing record of small birds may show that the emphasis on gigantism is somewhat artefactual.

The effects of human predation on the megafauna is much debated. In Australia it is suspected of having had a major influence on the extinction of these animals, but there is no direct evidence from middens (however, that dromornithids obviously had the attention of Australia's pre-European inhabitants is shown by cave paintings dating from 26 000 years BP). In contrast, the detrimental effects of human predation and habitat alteration on moas in New Zealand is well documented (Trotter & McCulloch 1984).

Many biogeographic studies have not considered fossil evidence of previous distributions. Overlooking evidence of major disruptions to many Pacific island avian communities by non-European humans can lead to serious underestimations of species richness (Steadman 1989). In Australasia there is evidence of such disruptions in New Zealand and New Caledonia. Historical biogeographic interpretations for taxa not usefully represented in the fossil record can be at best only tentative.

CONCLUSIONS

What can be said about the fossil record of birds in Australasia? Much is an indication of what it lacks. It is too patchy and uncoordinated between the major regional land masses to trace the connections among radiations, although the growing Pleistocene record in New Zealand, New Caledonia and Australia will permit an interesting comparative picture. Even in Australia, with its longer, richer record, some crucial times are not represented, although new sites, such as Murgon, will help fill these gaps.

There are critical geographical areas not represented, such as western Australia and most of New Guinea. There is an overwhelming need for accurately and directly dated sites. The taxonomic composition of the record is biased at certain times and certain localities. The waterbird-dominated record of Australia's Tertiary needs to be supplemented by non-aquatic taxa. The record of no group is rich enough in its taxonomic and chronological coverage for extensive phylogenetic studies, much less useful speculation on its origins.

Despite these deficiencies, the fossil record makes a useful contribution toward the understanding of Australasia's avifauna. It provides crucial documentation needed for building a broad picture of avian evolution on these southern land masses by documenting changing distributions and early faunal connections with other continents; questioning or corroborating previous ideas of Australasian endemism; testing theories on origins, colonisation routes and divergence times of various bird groups; and aiding the interpretation of changes in climate and environment. The record is still scanty, but will assume growing importance. Greater accessibility to known and future fossil localities, increased funding for field work and preparation, and the growing number of Australasian-based palaeo-ornithologists can not help but fruitfully build on the existing knowledge of the avian fossil record.

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BIOCHEMICAL EVIDENCE FOR THE ORIGINS AND EVOLUTIONARY RADIATIONS IN THE AUSTRALASIAN AVIFAUNA: THE SONGBIRDS

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ABSTRACT. DNA-DNA hybridization indicates that all Australasian-centred families of Passeriformes (songbirds) represent an endemic radiation, contrary to their conventional interpretation as diverse derivatives of Eurasian origin. Independent evidence based on protein electrophoresis is presented which corroborates many of the DNA findings but seriously calls into question the supposed links between Menuridae (lyrebirds), Ptilonorhynchidae (bowerbirds) and Climacteridae (treecreepers). The lyrebirds are isolated consistently as a sister lineage to the remaining Australasian songbirds. An apparently autochthonous radiation, confined largely to the Australo-Papuan continental plate, comprises the Acanthizidae (thornbill-warblers), Pardalotidae (pardalotes), Meliphagidae (honeyeaters), Epthianuridae (Australian chats), Eopsaltriidae (Australasian robins), Orthonychidae (logrunners) and, arguably, Maluridae (fairy-wrens). The biochemical results are also compared with data from microcomplement fixation. A Gondwanan origin for the Passeriformes is canvassed.

Keywords: Protein electrophoresis, biochemical evolution, phylogeny, passerines, songbirds, cladistic analysis, Australo-Papuan.

INTRODUCTION

Relationships of the Australo-Papuan songbirds (Passeriformes) have been the centre of much scientific interest following the DNA-DNA hybridization studies of Sibley and Ahlquist (summarized in Sibley et al. 1988). These identified a major dichotomy amongst the oscinine passerines: the Corvida which includes all the major Australo-Papuan lineages, and the Passerida which is centred in Eurasia (Figure 1). The Corvida itself comprised three primary lineages: the lyrebirds and allies (Menuroidea), the honeyeaters and allies (Meliphagoidea), and the crows, monarch flycatchers and allies (Corvoidea). The first two of these superfamilies are all but endemic to Australia-New Guinea, and the last, although almost cosmopolitan, is nevertheless most diverse in Australasia.

Although the results are exciting, concern has been raised regarding the reliability of the data and the methods of analysis. The lack of complete matrices, assumption of constant rate of molecular change, and limited tree building methodologies have all been points for criticism (see Mayr 1989, Sibley 1989, for recent commentary). One strategy to assess the results objectively is to compare them with those from other sets of data. To this end, the higher order relationships among Australo-Papuan songbirds are here examined by protein electrophoresis and, to a lesser extent, by the immunological technique of microcomplement fixation.

METHODS

Data from protein electrophoresis and microcomplement fixation were taken from the studies of Christidis and Schodde (1991) and Baverstock et al. (in press), respectively, and compared with the phylogenies derived from DNA-DNA hybridization (Sibley & Ahlquist 1985). In the electrophoretic study, allelic variation at 18 loci was examined by UPGMA, distance Wagner and PAUP procedures in 42 species (38 indigenous, 4 introduced of Australo-Papuan passerines, covering all 14 major elements of the Australo-Papuan-centred families and representatives of two to five families in each of the primary Eurasian assemblages as recognized by DNA-DNA hybridization (Sibley & Ahlquist 1985, Sibley et al. 1988). Here, the protein data are analyzed further by the HENNIG 86 cladistic program (Farris 1988) because it is particularly effective in finding the most parsimonious trees (Platnick 1989). In it, alleles were treated as characters and their presence or absence as states. Trees were outgroup rooted by the suboscine *Pitta*. The principal procedures used were mhennig* and tread with branch-breaking and successive weighting (Platnick 1989).

Microcomplement fixation data is taken from a series of oneway comparisons using one species from each of the Meliphagidae, Epthianuridae, Grallinidae and Climacteridae. Albumin antibody from the four was then compared against albumin antigens obtained from a number of species representing several other Australo-Papuan- and Eurasian centred families.

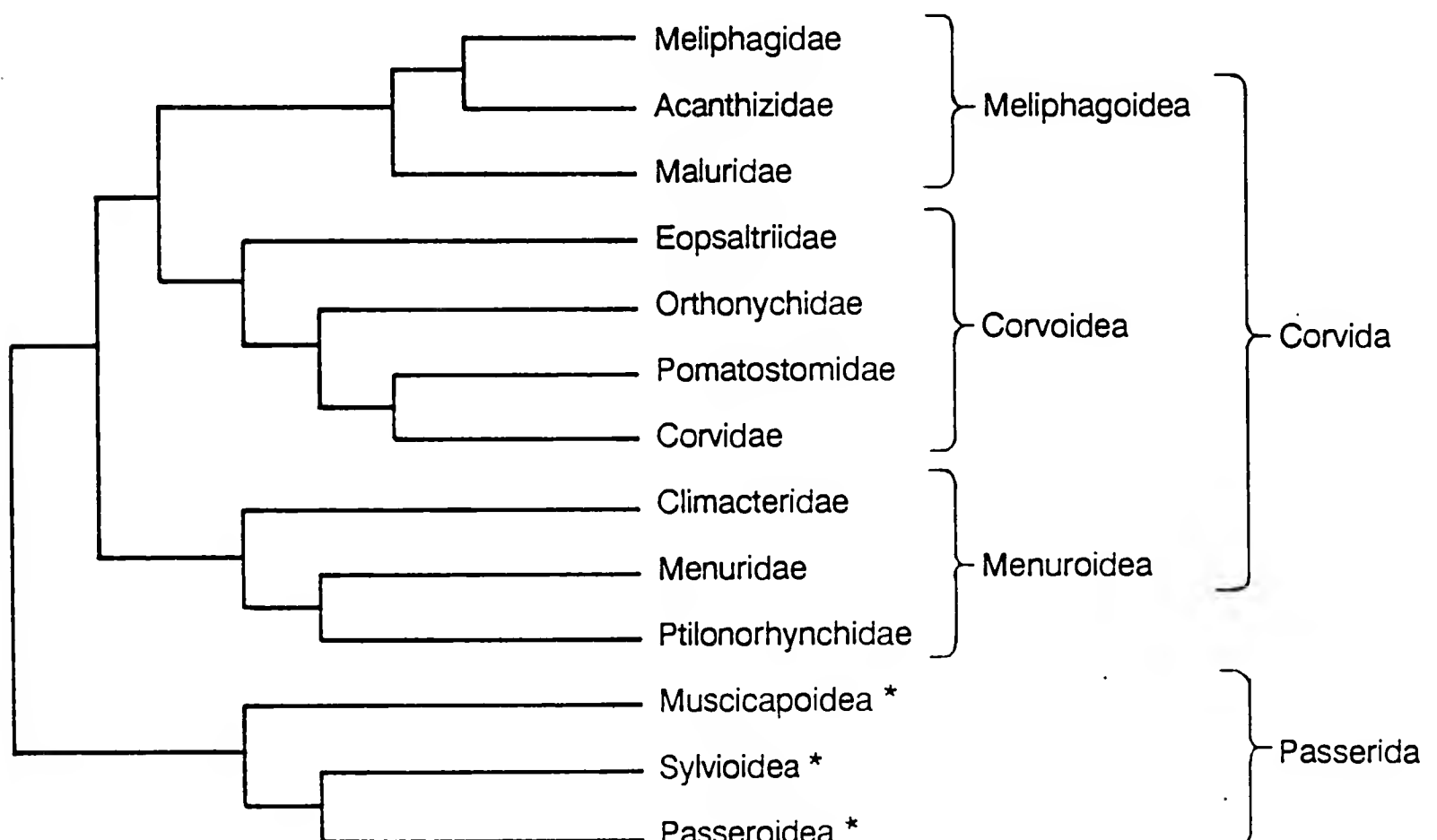


FIGURE 1 - Relationships of Australo-Papuan passerines as determined by DNA-DNA hybridization (based on Sibley & Ahlquist 1985). Only the 3 superfamilies within the Passerida are depicted and these are indicated by asterisks.

RESULTS

For the further cladistic analysis of electrophoretic data, the mhennig* procedure produced the most parsimonious trees; their consensus is depicted in Figure 2. Similar topologies were also produced for the major clades by the tread method. Both procedures separate the lyrebird (*Menura*) consistently as a sister group to the remaining songbirds. Several stepwise polychotomies and dichotomies follow, only a few of which are consistent between the trees derived from the two procedures. One that is

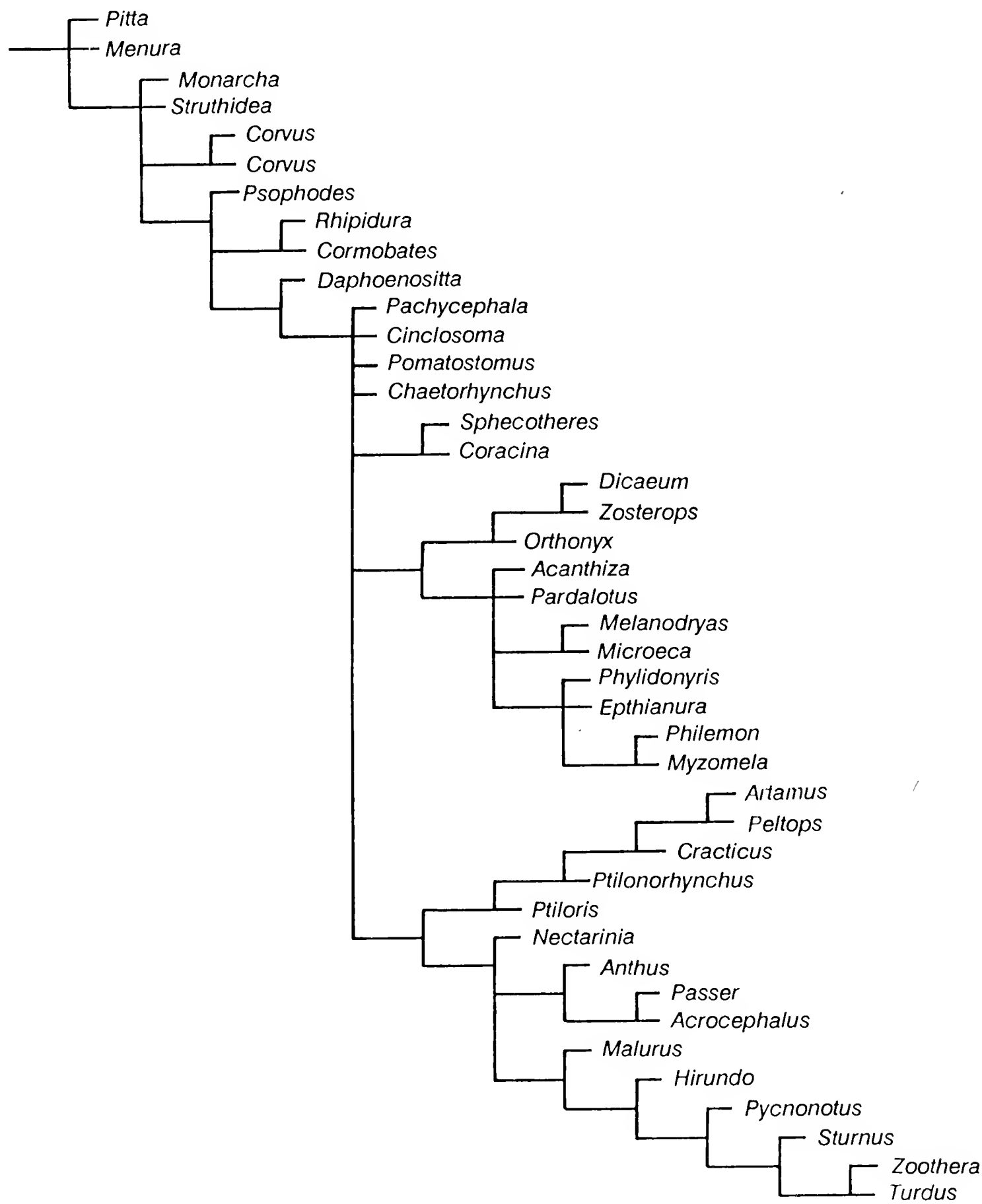


FIGURE 2 - Strict consensus tree derived from an analysis using the HENNIG program (Farris 1988) version 1.5, based on alleles as characters and their presence or absence as states. The mhennig* procedure with branch-breaking and successive weighting was employed.

comprises the meliphagine honeyeaters (*Myzomela*, *Phylidonyris*, *Philemon*), Australian chats (*Epthianura*), thornbill-warblers (*Acanthiza*), pardalotes (*Pardalotus*), eopsaltriine robins (*Microeca*, *Melanodryas*), logrunners (*Orthonyx*) and fairy-wrens (*Malurus*). A second assemblage encompasses Eurasian and African centred families included in the Passerida by DNA-DNA hybridisation (*Nectarinia* to *Turdus* in Figure 2). The Apostlebird, *Struthidea*, (Corcoracidae) is aligned with them anomalously only in the mhennig* tree. A third smaller assemblage comprising the butcherbirds (*Cracticus*), woodswallows and allies (*Artamus*, *Peltops*), bowerbirds (*Ptilonorhynchus*) and birds of paradise (*Ptiloris*) is identified by the tread procedure only. Microcomplement fixation distances within the Meliphagoidea, as identified in Figure 1, average 17. Those between the Meliphagoidea and both the Corvoidea and Menuroidea are around 25, and the Passerida are still further distant at values of 35 to 55.

DISCUSSION

The concept of an endemic radiation among the major Australo-Papuan-centred groups of songbirds is supported by protein allelic data and less forcefully by immunological distance. The Australo-Papuan robins (Eopsaltriidae), whistlers (Pachycephalidae), monarch flycatchers (Monarchidae), thornbill-warblers (Acanthizidae) are only distantly related to their supposed Old World counterparts in the Muscicapidae (*Turdus*) and Sylviidae (*Acrocephalus*). This is entirely consistent with DNA-DNA hybridization data (Sibley & Ahlquist 1985). So too is the separation of eopsaltriine robins from the whistlers, with which they have often been linked (Boles 1979). Moreover the association between the families Acanthizidae, Pardalotidae, Meliphagidae and Epthianuridae (Australian chats), identified by DNA-DNA hybridization studies (Figure 1), is shown also in the allelic and immunological data.

The data sets are, however, not congruent regarding the positions of the fairy-wrens (Maluridae), eopsaltriine robins and logrunner (*Orthonyx*) along the Australo-Papuan-centred families. Sibley and Ahlquist (1985) aligned the fairywrens with the Meliphagoidea (along with Acanthizidae and Meliphagidae) and recorded the latter two as outlying lineages of the Corvoidea. On allelic data, the eopsaltriine robins and logrunner are linked to the Acanthizidae and Meliphagidae instead. Their positioning of the fairy-wrens is just as ambivalent. Although the HENNIG analyses associated them with the Eopsaltriidae - Meliphagidae assemblage, this is not confirmed by PAUP and distance-based analyses (Christidis & Schodde 1991). However, microcomplement fixation supports the association between the Maluridae, Meliphagidae and Acanthizidae but data for the Eopsaltriidae is lacking.

The remaining Australo-Papuan songbirds included in the Corvoidea of Sibley and Ahlquist (1985) appear as an assemblage in the UPGMA and PAUP analysis of Christidis and Schodde (in press) but not in any of the protein-based HENNIG trees. There are also some differences between the DNA-based and protein-based topologies, particularly in the positions of *Cormobates* (Climacteridae), *Struthidea* (Corcoracidae), *Pomatostomus* (Pomatostomatidae), and *Ptilonorhynchus* (Ptilonorhynchidae). Nevertheless, both DNA-DNA hybridisation and allelic data align Oriolidae (*Specothes*) with Campephagidae (*Coracina*) and Artamidae (*Artamus*) with Cracticidae (*Cracticus*, *Peltops*). Moreover, microcomplement fixation results

confirm that the Magpie-lark *Grallina* is a monarch flycatcher (Monarchidae), distant from *Struthidea* and *Corcorax* (Baverstock et al. in press).

Although the Eurasian-centred families included in the Passerida of Sibley and Ahlquist (1985) appear to be closer to one another than to any Australo-Papuan-centred families, the clear cut separation between the Passerida (Eurasian centred) and Corvida (Australo-Papuan centred) is not as clear cut in the protein data. Nevertheless, microcomplement fixation data (Baverstock et al. in press) do to a limited extent support the separation between the Corvida and Passerida.

One significant area of discord between the allelic and DNA data sets involves the relationships of the lyrebirds (Menuridae), treecreepers (Climacteridae) and bowerbirds (Ptilonorhynchidae). The present protein data do not support their inclusion as a single superfamily as found by Sibley and Ahlquist (1985). Instead, *Ptilonorhynchus* (bowerbird) consistently clusters with the Cracticidae (butcherbirds), Artamidae (woodswallows) and Paradisaeidae (birds of paradise). Such a result is more consistent with morphological data (Bock 1963). *Cormobates* (treecreeper) has no obvious relatives, while *Menura* (lyrebird) is always isolated as a sister lineage to the remaining songbirds. Moreover, microcomplement fixation data also fails to align the treecreepers with the lyrebirds.

Despite conflicting evidence of relationships among these last three families, there is enough agreement between the DNA-DNA hybridization, protein and limited immunological data sets to substantiate the hypothesis of an endemic radiation amongst the Australo-Papuan passerines. Moreover, the Corvida can be separated into four assemblages. The first comprises the Acanthizidae, Paradalotidae, Meliphagidae, Epthianuridae, Eopsaltriidae, Orthonychidae and Maluridae. Two further assemblages are monofamilial and small: Menuridae and Climacteridae. These three assemblages are, with few exceptions, confined to the Australo-Papuan continental plate and can therefore be considered autochthonous. Judged by genetic distances (Christidis & Schodde in press) they appear to be descendants of the oldest branches of the songbird radiation. The final assemblage is equivalent to the Corvoidea (Sibley & Ahlquist 1985) including the Ptilonorhynchidae but excluding Eopsaltriidae and Orthonychidae. These families are more widespread and can be considered a link between the first three assemblages and the Passerida. Genetic distance data (Christidis & Schodde 1991) suggests that they, along with the Passerida, are of a more recent origin.

The framework outlined would argue against a Eurasian origin for the songbirds as a whole (cf. Wilson 1988, Mayr 1989). The meliphagine - eopsaltriine group along with the Climacteridae and Menuridae do not have links with the Passerida and appear to represent an early songbird radiation in Australasia. Of particular significance is the possible separation of the Menuridae as a distinct sister group to the remaining oscines. This is consistent with the conclusions of Feduccia and Olson (1982) based on morphological analyses. They suggest that the Menuridae represent the most primitive oscine lineage with links to the primitive South American suboscines, Rhinocryptidae. Such connections suggest that the relationships of the sub-oscine New Zealand wrens (Acanthisittidae) also need to be re-examined by protein electrophoresis and other techniques (cf. Raikow 1987).

From the divergences nearly uncovered among the passerines, a Gondwanan origin for the Passeriformes now becomes a plausible hypothesis with the order splitting

there in two major radiations: a sub-oscine radiation in western Gondwana (South America) and a primary oscine radiation in eastern Gondwana (proto-Australasia). The ancestors of the Passerida could then have spread into Eurasia and Africa where they underwent subsequent radiations. It is unclear as to whether the Corvoidea (as defined here) underwent their primary radiation in Australasia and then spread into Asia and Africa, or first radiated in Asia and then re-spread into Australasia. Support for a southern origin for the Passeriformes can also be found in the fossil record. Olson (1988) reports that passerines do not appear in the Northern hemisphere until the latest Oligocene and only become common in the Miocene but with no indication of an evolutionary origin.

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THE EVOLUTIONARY HISTORY OF PARROTS AND COCKATOOS: A MODEL FOR EVOLUTION IN THE AUSTRALASIAN AVIFAUNA

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ABSTRACT. The Psittaciformes represent a well-defined avian order that originated probably in the Australasian sector of Gondwana and which has had a long and independent evolutionary history leading to its present pan-austral distribution. Despite their unity in several fundamental characteristics, the Psittaciformes exhibit a great diversity of size, plumage, biology, ecology, and both external and internal morphology. This diversity has been explored from many sides in systematic studies through the application of a great variety of techniques and approaches. As a result, the systematics of the Psittaciformes has acquired the potential to provide the most corroborated classification of any Australasian avian order. Through the review and synthesis of data from the latest eco-geographical, functional-morphological and biochemical studies of parrots and cockatoos, the evolutionary history of the Psittaciformes will be constructed, both for its own sake and as a model for interpreting the evolution of other avian groups in the Australasian avifauna.

Keywords: Parrots, cockatoos, functional morphology, ecological morphology, ecological biogeography, biochemical systematics, Australasia, phylogenetic reconstruction.

INTRODUCTION

The Psittaciformes, which form the third-largest non-passerine avian order and have a broadly pan-austral distribution, display their greatest morphological and ecological diversity in Australasia. Representing an old avian lineage, they have demonstrated a remarkable propensity towards adapting to widely differing ecological conditions, while at the same time retaining a set of ancestral psittaciform characters. Hence, Psittaciformes form a clearly defined avian order that has (a) no marginal taxa that could suggest phylogenetic affinities to other avian orders; (b) numerous taxa that are relicts of early radiations, and the genealogical relationships of which have become obscured; and (c) many taxa resembling one another because of convergently acquired characters in response to similar environmental conditions.

In recent years, parrot systematics has shifted in focus from classifications based on similarities in standard characters as indicators of genealogical relationships towards the reconstruction of the evolutionary history. This reorientation was made possible by new developments in a variety of fields. Comparative functional morphology has provided a technique for distinguishing convergent characters from homologous ones and ancestral characters from derived states, thereby allowing the reconstruction of the evolutionary history of various characters (e.g., Glenny 1955, Homberger 1980, 1990, Guntert 1981, Homberger & Schodde in prep.). Biochemical systematics has generated new data for testing earlier hypotheses (e.g., Adams et al. 1984, Christidis et al. in press). Comparative ecological morphology of the feeding adaptations of parrots has also generated data that elucidate the nature of the linkage between the morphology of parrots and the ecology of their environment (e.g., Saunders 1974, Homberger 1990, unpubl. obs., Homberger & Schodde in prep.). Advances in the historical and ecological biogeography of Australasia, in their turn, have provided data

on the history of environmental changes and of associated changes in the geographical distribution of Australasian parrots (e.g., Schodde & Calaby 1972, Schodde 1982). In the following, three Australasian psittaciform taxa are selected as examples to illustrate how a synthesis of such data can improve our understanding of the evolutionary history of an avian order.

RESULTS

The Australasian true parrots

The true parrots (*Psittacinae sensu* Homberger 1980) of Australasia are usually divided into the platycercine (broad-tailed) and psittaculine (red-billed) parrots (e.g., Smith 1975; Homberger 1980). Four genera, however, are not easily classified as they show different taxonomic affinities according to the characters considered. These genera are *Alisterus* (king parrots), *Aprosmictus* (red-winged parrots), *Polytelis* (long-tailed parrots), and *Prosopeia* (shining parrots) (Homberger 1980).

Homberger (1980) provides a set of data and testable hypotheses as a basis for comparison with other studies. Based on functional-morphological characters of the feeding apparatus, *Alisterus*, *Aprosmictus*, and *Polytelis* were assigned to the psittaculine parrots. Furthermore, these three genera were found to share not only a unique lingual surface with *Eclectus* and some species of *Tanygnathus* (great-billed parrots) but also a derived condition of the soft palate with *Eclectus*, *Tanygnathus*, *Geoffroyus*, and *Psittacula* (ring-necked parrots). Thus, the Australo-Papuan genera *Eclectus*, *Alisterus*, and *Aprosmictus* were interpreted as having evolved from an oriental psittaculine stem and to have given rise, via an *Aprosmictus*-like ancestor, to the Australian *Polytelis*, of which Alexandra's Parrot *P. alexandrae* displays several uniquely derived characters. In contrast, *Prosopeia* was assigned to the platycercine parrots on the basis of functional-morphological characters of the feeding apparatus, and was shown to share numerous lingual and palatal characters with *Platycercus* (rosellas), *Cyanoramphus* (island parakeets), and *Eunymphicus* (horned parakeets). Because of the reduced surface structure of its hard palate, *Prosopeia* was interpreted as the Fijian end point of an evolutionary line that led from the Australian *Platycercus* via the Pacific *Cyanoramphus* to the New Caledonian *Eunymphicus*.

Güntert's (1981) data on the morphology of the proventriculus support the distinction between the psittaculine and platycercine parrots, but also show that *Prosopeia* has the most ancestral condition among the platycercine parrots. Like *Geoffroyus*, *Tanygnathus*, *Eclectus*, *Alisterus*, and *Aprosmictus*, it has also a very long intestine, which is an ancestral character within the Psittaciformes (Güntert 1981). Glenny's (1955) study on the aortic arch system shows that the A-1 carotid pattern, which is found in the above psittaculine parrots, is the ancestral condition, whereas the A-2-s carotid pattern, which is found in the above platycercine parrots, is derived.

The electrophoretic data by Christidis et al. (in press) support the close relationship among the platycercine parrots (in particular between *Platycercus* and *Cyanoramphus*) and between the psittaculine *Eclectus* and *Geoffroyus*. However, they depart from the data of the three previous studies by suggesting that *Alisterus* and *Polytelis* - as well as *Psittacella* (tiger-parrots) which is conventionally grouped with the psittaculine parrots - are more closely related to the platycercine parrots than to the psittaculine ones.

The biogeographical studies by Schodde & Calaby (1972) and Schodde (1982) show that birds with a present-day Tumbunan distribution in the rainforests of montane New Guinea and coastal eastern Australia are remnants of an avifauna that lived and diversified in subtropical rainforests that covered most of Australia in mid-Tertiary times. This Tumbunan avifauna has been a reservoir for several more derived avifaunae: the Irian avifauna of the rainforests of lowland New Guinea and Cape York Peninsula, and the northern Torresian and southern Bassian avifaunae of wet sclerophyll forests and woodlands in Australia. The Eyrean avifauna of arid central Australia developed largely out of the Bassian avifauna, especially its western part.

None of the above sets of data is complete and none of the resulting interpretations is final. But a synthesis of all of the above data can nevertheless provide an evolutionary scenario that may well bring us a step or two closer to the true phylogeny of parrots.

Alisterus, having a Tumbunan distribution, is probably a descendant of a Tertiary rainforest-dwelling psittaculine ancestor from which it retained the ancestral A-1 carotid pattern and long intestine, as well as the already derived lingual surface pattern and soft palate configuration. From such an ancestor, *Eclectus* is likely to have evolved by entering the Irian rainforests and by changing little, except its plumage. *Geoffroyus*, *Tanygnathus*, and *Psittacula* probably branched off the psittaculine stem separately from one another and before *Eclectus* did, as is suggested by their various ancestral features in the feeding and digestive systems. *Psittacula* has had the longest independent evolution as is suggested by electrophoretic data and the derived characters in its digestive tract. An *Alisterus*-like ancestor also gave rise to two other lineages: *Aprosmictus* in the Torresian north and *Polytelis* in the Bassian south (Schodde 1982). In its turn, the latter gave rise to the Eyrean *Polytelis alexandrae* (Schodde 1982) which displays many adaptations to its arid environment (Homberger 1980, Güntert 1981).

That the present-day platycercine parrots may also have evolved from a Tertiary, rainforest-dwelling ancestor, which had not diverged much yet from the psittaculine ancestor, is suggested not only by the electrophoretic data which postulate a closer relationship between *Alisterus* and the platycercine parrots - but also by *Psittacella*. This Tumbunan genus has an ancestral A-1 carotid pattern (Smith 1975) and is presently restricted to montane New Guinea. Its platycercine affinities are suggested not only by electrophoretic data but also by its plumage (Güntert 1981, Schodde *in litt.* 1988, Christidis et al. in press). The only other platycercine parrots with an A-1 carotid pattern are the Australian genera *Melopsittacus* (Budgerigar), *Neopsephotus* (Bourke's Parrot) and *Neophema* (grass parrots), which are thought to have branched off the main platycercine stem at an early stage of its evolution and adapted to arid conditions (Homberger 1980, Schodde 1982, Christidis et al. in press).

The rainforest-dwelling platycercine ancestor then acquired the derived characters of the feeding apparatus that are shared by its present-day descendants (see below), but must have had retained a long intestine. The blue-cheeked rosellas (i.e., *Platycercus elegans* and *P. caledonicus*) in the rainforests and woodlands of Eastern Australia and Tasmania, respectively, represent one branch that may not have changed much from the ancestral stem, though it acquired a shorter intestine and also gave rise to several more arid-adapted species (Schodde 1982). *Cyanoramphus* is another branch

which may have changed little as it spread over the islands of the Tasman Sea and Pacific Ocean, though it also acquired a short intestine and a reduced surface pattern on the hard palate (Homberger 1980, Güntert 1981, Christidis et al. in press). The New Caledonian *Eunymphicus* may have evolved from a *Cyanoramphus* like ancestor, from which it diverged little apart from a further reduction in the surface pattern of its hard palate and some modification to its plumage (Homberger 1980, Güntert 1981, Rinke 1989a), even so, a direct derivation from a rainforest-dwelling platycercine stem cannot be discounted at this point.

Prosopeia is unlikely to have evolved directly from an *Eunymphicus*-like or *Cyanoramphus*-like ancestor (cf. Homberger 1980, Rinke 1989a). Because of its long intestine and more primitive proventriculus (Güntert 1981), it must have branched off an early *Cyanoramphus* or *Eunymphicus* stock that still had retained these ancestral characters or have arisen directly from the rainforest-dwelling platycercine stem. In either case, *Prosopeia* seems to have changed little from its immediate ancestor; but, given that the Fijian avifauna is derived from Papuasia (see Rinke 1989a), the direct derivation of *Prosopeia* from a northern Australo-Papuan rainforest-dwelling platycercine stem would make it less of a zoogeographical puzzle. Its plumage characters, which indicate a temperate ancestry (Rinke 1989b), are inconclusive.

The Australasian cockatoos

Cockatoos form a distinct group (Cacatuidae) within the Psittaciformes and are restricted to Australasia (e.g., Smith 1976, Homberger 1980, Adams et al. 1984), but their intrafamilial relationships have been little understood until recently.

Glenny (1955, *in litt.* 1990) showed that the ancestral A-1 carotid pattern is found in the black cockatoos (*Calyptorhynchus* spp.), the Palm Cockatoo (*Probosciger aterrimus*), the Gang-gang Cockatoo (*Callocephalon fimbriatum*), the Galah (*Eolophus roseicapillus*), and the Cockatiel (*Leptolophus hollandicus*), whereas the derived unicarotid B pattern is found in all other species (*Cacatua* spp.). Dyck (1977) also found that cockatoo feathers lack a spongy ultrastructure and, therefore, lack blue, green and purple colours.

The electrophoretic data of Adams et al. (1984) confirmed the monophyly of the *Calyptorhynchus* species and identified *Leptolophus* as an early offshoot from the cockatoo stem, but were unable to resolve the phylogenetic positions of *Callocephalon*, *Eolophus*, *Cacatua galerita* (Sulphur-crested Cockatoo), and *Cacatua leadbeateri* (Pink Cockatoo).

On the basis of skull characters, Baird (1985) was able to separate *Cacatua* from *Calyptorhynchus* and *Callocephalon*. The study of skull characters by Homberger & Schodde (in prep.) confirmed this division, but also revealed similarities between *Calyptorhynchus* and *Leptolophus*, between *Callocephalon* and *Eolophus*, between *Callocephalon* and the red-tailed black-cockatoos (*Calyptorhynchus banksii* and *C. lathamii*), and between *Calyptorhynchus banksii* and *Probosciger*.

My own eco-morphological data (Homberger 1990, unpubl. obs.) reveal that *Callocephalon* and most species of *Calyptorhynchus* (except *C. banksii samueli*) display at least four of the five following ancestral psittaciform characters: arboreality, a pincer-like bill, a lack of filing ridges on the inner surface of the upper bill tip, poor

seed-shelling ability, and a diet of significant proportions of wood-boring or gall-forming insect larvae. In contrast, all the other cacatuid genera, as well as *Calyptorhynchus banksii samueli*, are characterized by the following derived, but often convergently acquired characters: filing ridges and a transversal step on the inner surface of the upper bill tip, a projecting upper bill tip, the use of the lower mandible as the instrumental part of the jaw apparatus, an excellent seed-shelling ability, and a diet of mainly seeds.

A synthesis of the above data with biogeographical information suggests the following evolutionary history of cockatoos.

Calyptorhynchus, *Callocephalon*, and *Probosciger* evolved probably from a Tertiary, subtropical rainforest-dwelling *Calyptorhynchus*-like ancestor which had retained several proto-psittaciform characters, such as the A-1 carotid pattern, a lack of blue-green feather colours and a pincer-like bill that was used primarily to extract wood-boring or gall-forming insect-larvae. Today, no cacatuid descendants survive in subtropical rainforests. *Calyptorhynchus* and *Callocephalon* may have changed little, except in the morphology of their feeding apparatus, the present diversity of which is the result of different adaptations towards seed predation. Most species entered and remained tied to the Bassian forests and woodlands, except for some subspecies of *Calyptorhynchus banksii*, which entered the Torresian woodlands, and for *Calyptorhynchus banksii samueli*, which adapted to the arid Eyrean region by becoming more terrestrial and granivorous.

Probosciger aterrimus, which has an Irian distribution, is probably a descendant of a Papuan population of the dark plumaged ancestral calyptorhynchid stem and has become a specialized seed-predator of large tree fruits. The Eyrean *Leptolophus* is probably derived from an early *Calyptorhynchus*-like ancestor, while *Eolophus* and *Cacatua leadbeateri* are more likely to have evolved from a *Callocephalon*-like ancestor, though independently from each other. The origins of the typical white cockatoos are still unclear, but they comprise two separate lineages: The black-billed white cockatoos (i.e., *Cacatua galerita*, *C. sulphurea*, *C. moluccensis*, *C. alba*) and the white-billed cockatoos or corellas (e.g., *Cacatua sanguinea*, etc.). All these lineages probably have acquired their seed-shelling specializations independently of each other. *Eolophus* and the Australian representatives of the corellas and of *Cacatua galerita* have become adapted secondarily to exploit nutritious plant parts in or on the ground as well.

Thus, the present diversity in cockatoos comprises largely the remnants of separate, early radiations from a central pool of forest-dwelling *Calyptorhynchus*-like ancestors towards more granivorous, arid-adapted, and terrestrial forms.

The Papuan Pesquet's Parrot (*Psittrichas fulgidus*)

The Pesquet's Parrot has diverged so far from all other Psittaciformes that its origin and phylogenetic relationships have become obscure. It clearly evolved from a seed-shelling ancestor, but has become frugivorous and has acquired the derived A-2-s carotid pattern (Glenny 1955, Homberger 1980, Guntert 1981). Because its feathers lack a spongy ultrastructure, Dyck (1977) suggested that *Psittrichas* and the cockatoos may have evolved from a common ancestor that had diverged from the main psittaciform stem before the evolution of a spongy ultrastructure in the feathers. Yet *Psittrichas* does not resemble the cockatoos in any way except in plumage, so that

its ancestor had probably already diverged from the Tertiary rainforest-dwelling ancestor that gave rise to the cockatoos. This fits its present distribution, for *Psittarchas* occurs in the hill rainforests in New Guinea where many mid-Tertiary Tumbunan relicts survive today.

CONCLUSIONS

This reconstruction of the phylogeny of three Australasian psittaciform taxa suggests that the Psittaciformes radiated out of the subtropical rainforests of the Australasian sector of Gondwana. It also supports a well-established hypothesis that parrots evolved from an arboreal ancestor, because they are characterized by a zygodactylous foot and white egg shells, and because they usually nest in tree holes.

Given the great difficulties and possible pitfalls inherent in any systematic study, but especially in a study of an old group with a poor fossil record, systematics will have to depend increasingly on collaborative, multi-disciplinary and non-dogmatic approaches rather than on the use of single character complexes, techniques or methods to unravel the evolutionary history of birds.

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THE DEVELOPMENT OF MODERN AVIFAUNULAS

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ABSTRACT. The development of the Australasian avifauna until its modern speciation is explored by area cladistic analysis and phylogenetic relationships among marker taxa. Eight basic avifaunal elements are identified, all autochthonous except for the New Guinean alpine element. Comparison of the present structure and distribution of these elements against regional palaeogeography leads to the following reconstructions. The minor New Zealand and New Caledonian elements comprise a limited Gondwanan base, augmented by extensive colonization from Australia-New Guinea. Australia and New Guinea share a common avifaunal history rooted in a subtropical rainforest (Tumbunan) faunula widespread in Australia through the mid Tertiary. The dessication of Australia and raising of the New Guinean cordillera at the close of the Tertiary caused the Tumbunan faunula to withdraw to east coastal and montane refuges and spurred radiation of its elements adapting to tropical rainforest and scleromorphic vegetation.

Keywords: Australasian avifauna, causal biogeography, cladistic analysis, phylogenetic radiation, faunal elements, palaeogeography.

INTRODUCTION

Core Australasia comprises the east Gondwanan fragments of Australia, New Zealand, New Guinea and New Caledonia. The bird faunas of these fragments have much more in common with one another than with those of any other continent: a suite of closely allied ratites (*Dromaius*, *Casuarus*, *Apteryx*), a diversity of parrots and cockatoos, primitive songbirds linked to the oscines (*Menura*, *Atrichornis*, *Xenicus*), and a dominance of honeyeaters, monarchine flycatchers and acanthizid warblers among passerines. It is this distinctive structure that binds the Australasian avifauna into a single regional unit, one formed from the same sources.

From its origins to its speciation today, this avifauna has undergone long and involved radiations, invasions and extinctions, the courses of which have never been traced in any comprehensive way. Instead, ornithogeographers have relied on presumed source stocks and recent speciation for describing regional bird geography (Mayr 1944, Falla 1953, Kikkawa & Pearse 1969, Diamond 1972, 1985, Cracraft 1973, 1986, Bull & Whitaker 1975, Keast 1981, Pratt 1982, Ford 1987). What developed in between, from the earlier mid Tertiary? What were the regional elements from which the avifauna of today radiated? Where do they survive? When and how did they diverge from one another? These are questions of pattern which, both spatial and temporal, need resolution before the processes assembling the present Australasian avifauna can be appreciated fully.

METHODS

In the absence of a comprehensive fossil record (Boles, this symposium), clues for tracing faunal development come from residual zoogeographical pattern. Two

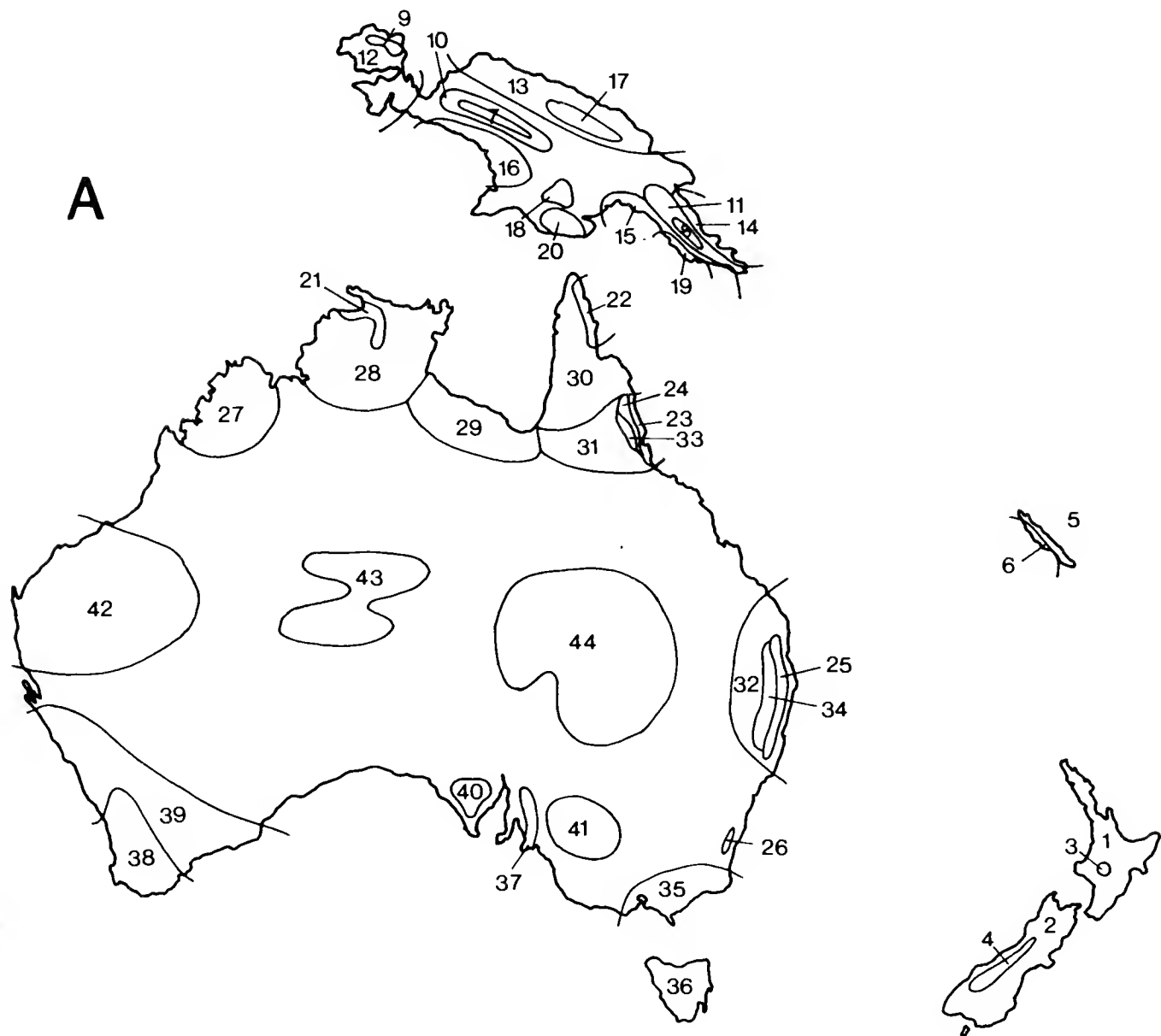


FIGURE 1A - Regional habitats sampled for avifaunal comparison: 1-2, New Zealand sub-tropical rainforest and stream-sides; 3-4, New Zealand alpine moor; 5, New Caledonian rainforest and maquis; 6, New Caledonian paperbark (*Melaleuca*) savannah; 7-8, New Guinean alpine moor; 9-11, New Guinean montane rainforest above 1500 m a.s.l.; 12-16, New Guinean lowland rainforest below 500m a.s.l.; 17-18, New Guinean swamp grassland; 19-20, New Guinean tropical eucalypt woodland; 21-23, Australian tropical rainforest (including mangroves); 24-26, Australian subtropical rainforest; 27-32, Australian tropical eucalypt woodland; 33-38, Australian temperate/tableland eucalypt forest and heath; 39-41, Australian mallee; 42-44, Australian desert ranges/basins...

approaches to determine it are combined here. One assesses biogeographic congruence among faunal assemblages; the other unravels phylogenies of taxa on a geographic base. Our assessment of assemblages attempts to identify the major avifaunal elements in Australasia. That of phylogeographic radiation in taxa is extrapolated to explore how those elements are related to one another.

Our regional assemblages are drawn from the regional ornithogeographies and check-lists of Kinsky (1970) and Bull and Whitaker (1975) for New Zealand, Delacour (1966) for New Caledonia, Pratt (1982) and Beehler and Finch (1985) for New Guinea, and Condon (1975), Schodde (1975, 1982a) and Ford (1987 and references therein) for Australia. To avoid the typological constraints identified by Vuilleumier (1975), the assemblages are habitat-based and limited to species that breed *in situ* and occur on

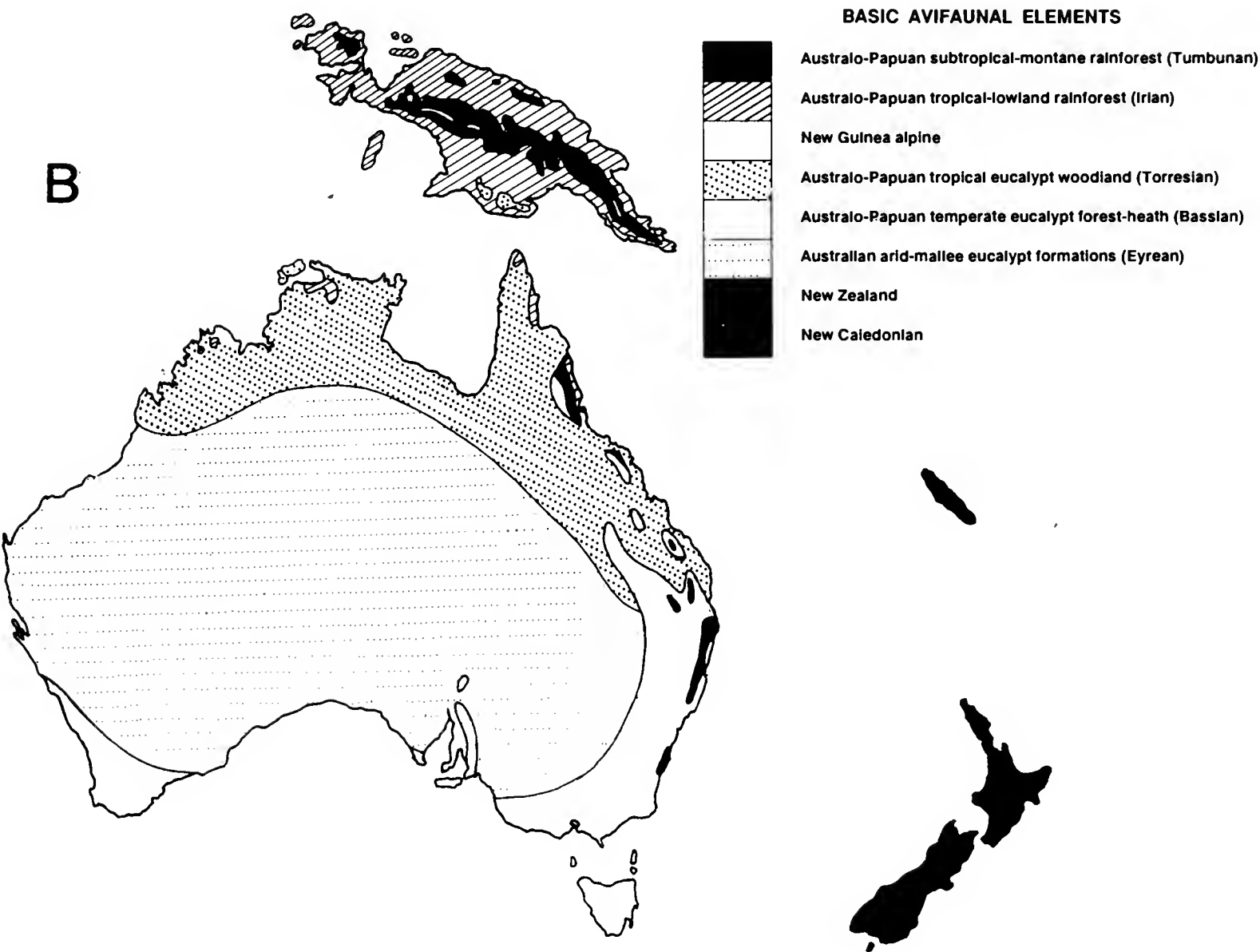


FIGURE 1B – Basic avifaunal elements of Australasia and their present distribution.

land and the land edge of freshwater. Only major natural habitats were used for delimiting assemblages, eight being identified as representative for Australasia : subtropical-montane rainforest, tropical lowland rainforest, alpine moor, tropical eucalypt woodland, temperate-montane eucalypt forest-heath, eucalypt mallee, swamp grassland, and desert formations. Component taxa were then scored for each habitat in 44 areas throughout the region to ensure that all significant centres of endemism were covered and that habitats were replicated regionally (Figure 1, caption). Genera and species were examined separately to add a temporal dimension. In all, 338 genera and 918 species were included, covering 96% and 94% respectively of Australasian breeding land and freshwater birds.

To assess the relationships among regional assemblages, the component taxa from all sample areas were compared by two hierarchical procedures, one phenetic, the other cladistic. The phenetic program, UPGMA (as in PATN, Belbin 1987), employed Manhattan distances; in clustering areas according to overall similarity, it is biogeographically neutral insofar as it does not weight vicariance and dispersal over one another. The two cladistic packages used, PAUP version 3.0 (Swofford 1990) and Hennig 86 version 1.5 (Farris 1988), stress shared-presence of taxa in grouping areas and employ parsimony to discriminate among vicariant explanations for the data. Because there is at present no indisputable outgroup for the regional assemblages, the area cladograms produced were not rooted.

As a result, the cladograms provide no firm indication of ancestry and derivation among faunal assemblages. For tracing this, we drew evidence from phylogenetic case histories published for autochthonous marker taxa that have speciated in all or most of the presumed avifaunal elements in Australasia.

RESULTS

Although the UPGMA phenogram for genera grouped the 44 assemblages into clusters largely consistent with previous descriptive studies (e.g. Schodde 1982a) and the cladistic analyses (Figure 2), that for species produced absurd associations. Options (e.g. 'B = -0.1', Belbin 1987) to tighten the clusters produced large changes in topology indicative of instability. Accordingly the UPGMA analyses were discarded.

Both cladistic programs for genera produced five equally short trees of 844 steps (consistency index 0.39) and identical topology. A strict consensus tree derived from the PAUP cladograms is presented in Figure 2, in which terminal branches for indisputably close sister assemblages have been collapsed for better appreciation. The New Zealand rainforest and New Guinean and New Zealand alpine assemblages are separated first as outlying elements. Then the New Guinean swamp grassland component is split off, along with all Australo-Papuan and New Caledonian rainforest assemblages on one side and those of the Australian eucalypt or scleromorphic vegetation on the other. Significantly for rainforest elements, those in montane New Guinea cluster with Australian subtropical assemblages, and those in tropical Australia with lowland New Guinea.

The assemblages of scleromorphic vegetation are aligned as follows: New Guinean tropical with Australian tropical, then a cluster comprising the temperate assemblages of southern and montane eastern Australia, which are linked in turn to those of the Australian mallee and arid zone. There is one noteworthy anomaly. The north Queensland tableland assemblage, which includes many temperate species, is linked more closely to the tropical assemblages than the lowland central east coast assemblage which itself includes many tropical-centred species. When their branches are reversed, the tree is lengthened by only two steps.

For species, only HENNIG 86 coped with the vast matrix of 918 species partitioned among 44 areas. It produced six equally short trees of 1733 steps (consistency index 0.51). A strict consensus tree derived from them, in which terminal branches for close sister assemblages have again been collapsed, is presented in Figure 2. It is little different in topology from the tree for genera, the Australo-Papuan rainforest and scleromorphic vegetation elements separating once more, and the New Zealand and New Caledonian assemblages lying further out. The only noteworthy variations are the linking of Australian subtropical rainforest assemblages to those in tropical Australia instead of montane New Guinea; and the clustering of the north Queensland tableland eucalypt assemblage now with temperate or Bassian elements.

Autochthonous Australasian marker taxa that have speciated through all or most regional avifaunas are few and limited largely to Australo-Papua; and those that have been assessed phylogenetically are still fewer. Among all there is a consensus that rainforest-inhabiting members, particularly in montane New Guinea and subtropical Australia, represent ancestral forms from which those in scleromorphic vegetation

AUSTRALIAN AVIFAUNAL ASSEMBLAGES

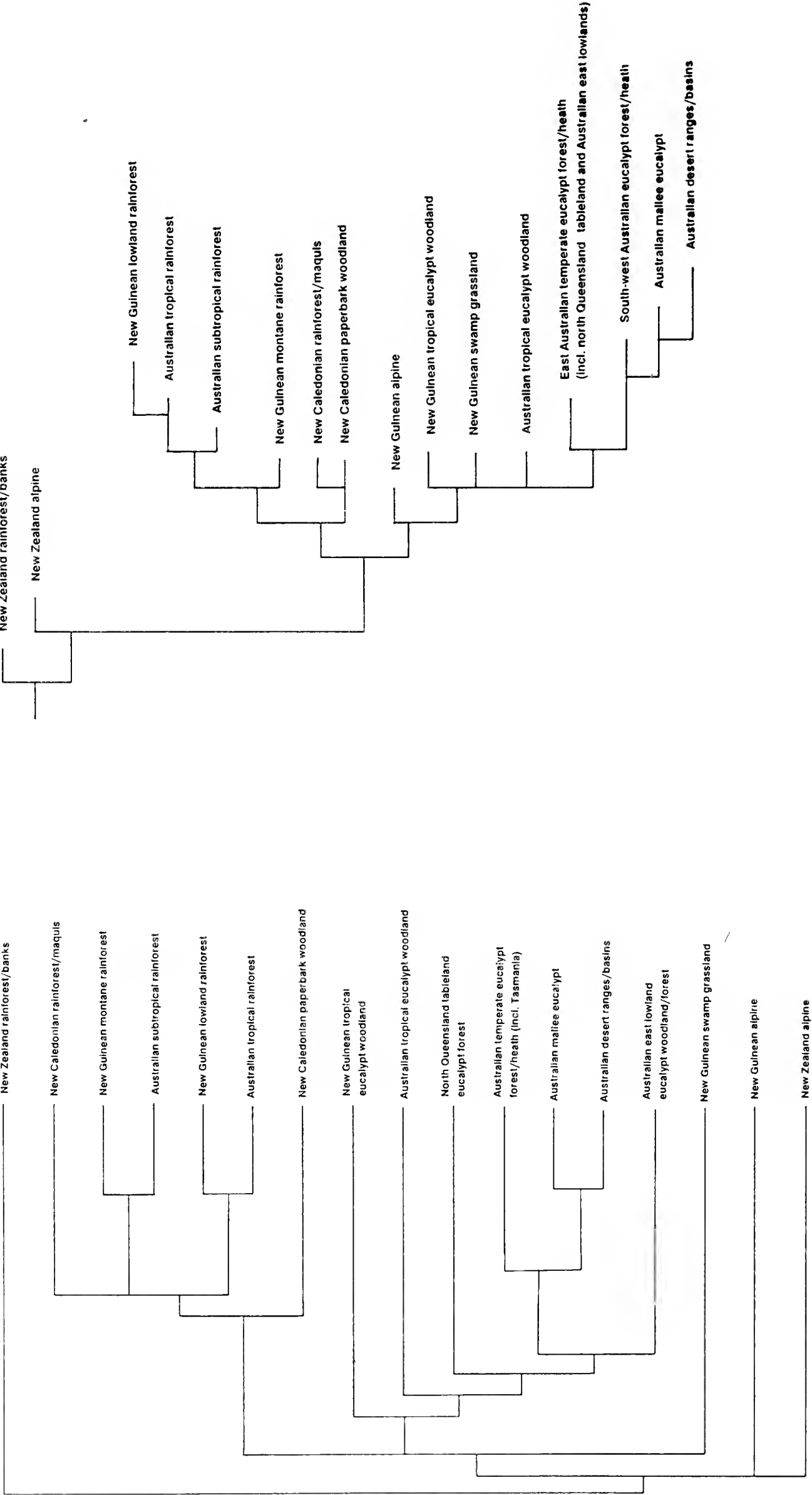


FIGURE 2 – Caption next page.

have been derived. This has been found in the bronze-cuckoos, *Chrysococcyx* (Marchant 1972), and in the Australo-Papuan thornbills, scrubwrens, robins and fairy-wrens, *Acanthiza*, *Sericornis*, *Petroica*, *Malurus* (Mayr & Serventy 1938, Christidis et al. 1988, Fleming 1950, Schodde 1982b). The single exception, stressed by Ford (1986) in acanthizid *Gerygone*, is a misinterpretation. Although Ford found no evidence for a subtropical rainforest (Tumbunan) origin, his two ancestral species-groups, *Gerygone mouki* and *G. fusca*, are respectively core elements of the subtropical rainforests of Australia-New Zealand and represented by a root member, *Gerygone ruficollis*, in montane New Guinea.

DISCUSSION

Synthesis of ornithogeographical elements

The congruence between the area cladograms for genera and species with descriptive ornithogeographies (e.g. Schodde 1982a) is consistent with a long history of endemic vicariant development in the Australasian avifauna. This is particularly so for Australia-New Guinea, exploding misconceptions still current in the Australian literature. Australia and New Guinea are not twin faunas (cf. Keast 1981); they share the same avifauna split fortuitously at Torres Strait by global climate. Its rainforest facet dominates in New Guinea and its scleromorphic vegetation facet in Australia, but outliers of both are present vicariously in both lands. Any ornithogeography which does not distinguish them in Australia is flawed (cf. Kikkawa and Pearse 1969). The avifaunas of New Zealand and New Caledonia, and of the limited environments of swamp grassland and alpine moor, are more distantly divergent and ambivalent in their links. Judged by their depauperate composition, they are built largely by dispersive taxa.

Because of the age of its members, the area cladogram of generic assemblages probably represents basic Australasian avifaunal elements the better. When paired Australian and New Guinean assemblages are grouped and extrapolated through their vegetational environments today, eight major avifaunal elements result with a distribution as given in Figure 1. The five largest approximate closely to the Tumbunan, Irian, Torresian, Bassian and Eyrean avifaunulas already identified in earlier empirical studies (Schodde 1982a and references therein), and are shared by Australia-New Guinea. The other three are the New Guinean alpine and New Zealand and New Caledonian elements. Significant endemism is characteristic of all eight; lack of it discounted the New Guinean swamp grassland fauna.

Reconstruction of avifaunal development

From their structure and links, the likely development of these avifaunal elements can now be traced on a palaeogeographical base. The small disharmonic New Zealand avifauna is layered in character, comprising a Gondwanan base upon which successive waves of immigrants, mostly from Australia, have built (cf. Fleming 1962). The

FIGURE 2 - *Left*. Strict consensus area cladogram of Australian avifaunal assemblages for genera, based on five PAUP trees produced using the procedures "Heuristic search, Hold = 5, Addition sequence = simple, Heuristic search with addition sequence = random", and "TBR" branching swapping. *Right*. Strict consensus area cladogram of Australian avifaunal assemblages for species, based on six HENNIG 86 trees produced using the procedures "mhennig*" and "bb*" to apply extended branch swapping.

Gondwanan base – of kiwis, the recently extinct moas, nestorine parrots, and perhaps the xenicid wrens – is unique. Initial Tertiary immigrants probably included the ancestors of cyanoramphine parrots, mohouines, crow-honeyeaters and callaeatids. Last to arrive were members of modern Australian genera and species, establishing themselves in Gondwanan rainforests that have changed little since the mid Tertiary and been culled to an uncertain extent by tectonic events and Pleistocene glaciations.

With 71 species, New Caledonia also has a small and disharmonic avifauna, in marked contrast to its continental flora rich in Gondwanan elements. The only likely living Gondwanan relict is the Kagu, *Rhynochetos jubatus*. Nearly all other avian taxa are of genera and species widespread in Australia-New Guinea and New Zealand today, indicating that the New Caledonian avifauna too has been built by dispersal, principally from Australian and New Guinean centres. Generic endemism is less than in New Zealand and there is little faunal layering, suggesting a later, more compressed history of colonization.

The development of the great, harmonic Australian and New Guinean avifaunas, which today share 900 of the breeding land and freshwater birds in the region, is reconstructed here together because their lands have a common palaeogeographical history and share a rich Gondwanan base of ratites, megapodes and Psittaciformes, and possibly ground pigeons, tytonid owls, podargids, wood kingfishers and even passerines. By the mid Tertiary, New Guinea had not formed. Its present southern plain was part of the northern rim of the stable Australian plate and its northern sector a skein of fringing islands. Australia itself was vegetated extensively with subtropical rainforests that included Gondwanan laurels, myrtles, podocarps, cunoniads and Antarctic Beech (*Nothofagus*) found in montane New Guinea today (Kemp 1978; Barlow 1981). This correlation suggests that the subtropical, Tumbunan avifaunas now present in montane New Guinea were widespread in Australia then. The north New Guinean islands, in contrast, appear to have been clothed in rich rainforests of Malesian origin (Axelrod & Raven 1982).

Two coincident events from the later Tertiary into the Pleistocene shaped subsequent developments. One was the raising of the massive central New Guinean cordillera to join the northern islands with the southern plain; New Guinea took its present form from then on (Pieters 1982). The other was the onset of aridity in Australia (Bowler 1982). The austral rainforest biota evidently withdrew before it, taking refuge ultimately in humid pockets on east coast ranges and in montane New Guinea. As Archer and Fox (1984) paraphrase, a walk up a New Guinea mountain is a walk back into time. On the caps of the New Guinean cordillera developed a novel alpine moor, opening new niches colonized itinerantly more by dispersing Eurasian taxa – phasianids, thrushes, pipits and munias – than Australian elements.

The tropical Malesian rainforests of the north New Guinean islands now spread south around the cordillera into far northern Australia, to be occupied primarily by birds of Australian origin. This biogeographical paradox, which holds for mammals as well, still needs a full accounting (Gressitt 1982).

In Australia itself, intensifying aridity spurred a radiation in already incipient scleromorphic vegetation avifaunas (cf. Kikkawa et al. 1979; Barlow 1981). These drew their ancestral stocks mainly from autochthonous rainforests through adaptation

(Schodde 1982a). Regional topography and climatic pattern focussed aridity in the centre of the continent, in effect splitting the avifaunas of eucalypt forests and woodlands into northern tropical (Torresian) and southern temperate (Bassian) belts. There they have since diverged from one another, as is evident in many vicariant pairs of taxa at generic (e.g. *Geophaps* - *Phaps*, *Aprosmictus* - *Polytelis*) and species (e.g. *Melithreptus albogularis* - *M. lunatus*, *Artamus minor* - *A. cyanopterus*) level. The arid centre itself drew its fauna from Bassian (primarily) and Torresian sources, building on trains of adaptive shifts that were culled repeatedly by climatic oscillations into the Pleistocene (Schodde 1982a). The scene had now been laid for the modern regional speciation documented so ably in current taxonomic literature.

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CONCLUDING REMARKS: ORIGINS AND EVOLUTION OF THE AUSTRALASIAN AVIFAUNA

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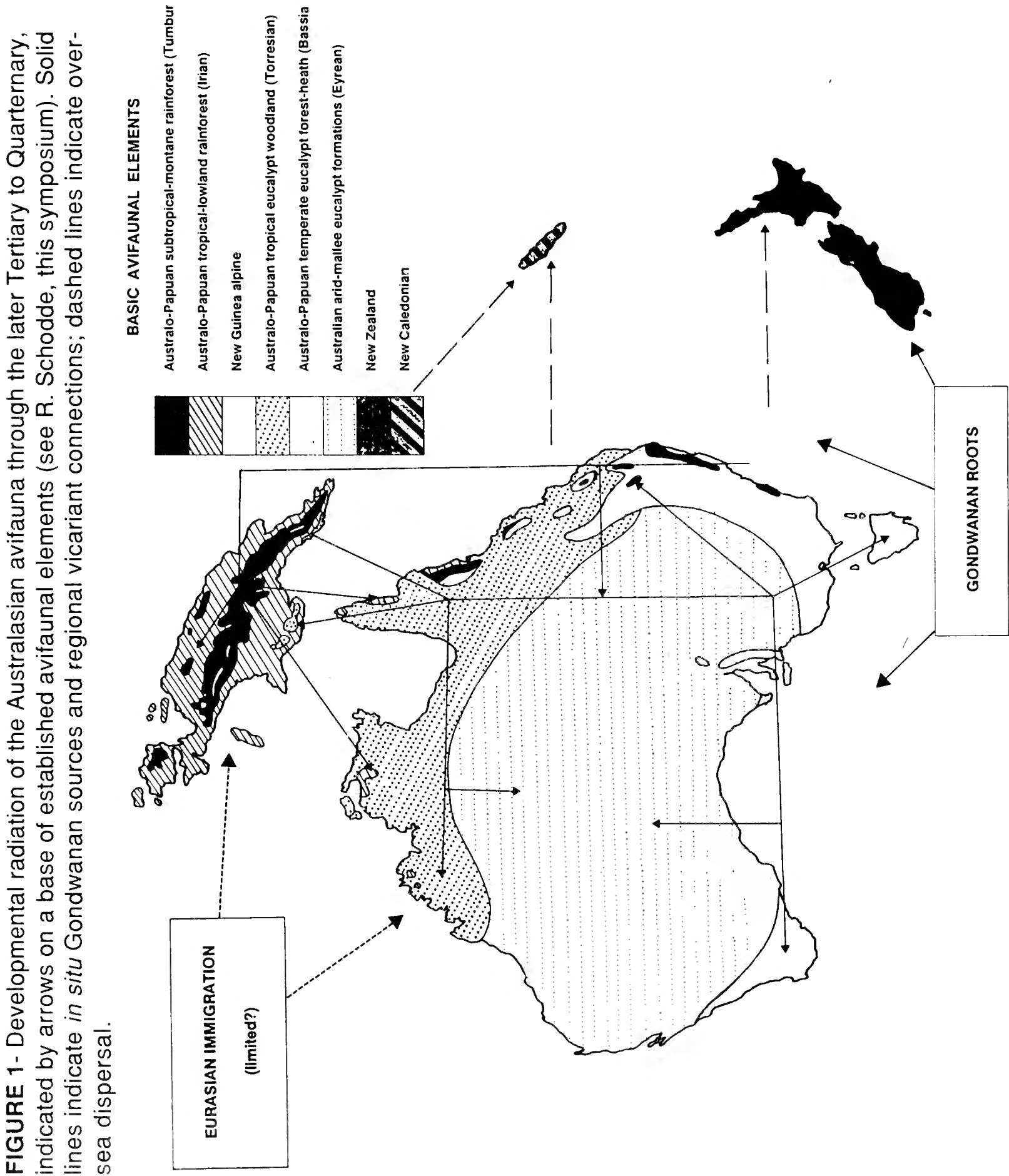
It is my personal pleasure to open my concluding remarks by dedicating this symposium to the late Australian systematic ornithologist, Dr Julian Ralph Ford. Julian Ford died in tragic circumstances at the age of 54 only months after attending the last Congress in Ottawa. Just as distressingly, the root cause - sectional antipathy to collecting, no matter how carefully planned - still remains. A driving man, Julian Ford had a meteoric effect on systematic ornithology in Australia in his 25 years of involvement, rising to become the leading exponent of geographical variation and speciation in Australian birds.

The principal contribution that symposia such as this make to hypothetical faunal origins is their up-dating of perception in the light of current knowledge. Advances in perception, in their turn, can only be judged from comparison with earlier reconstructions. The last coherent syntheses of origins and radiation in the Australasian avifauna were brought together by Ernst Mayr (1944, 1965) and Allen Keast (1961, 1981) through the 1950s to 1970s. They saw the Australasian avifaunas as built up by immigrant dispersal from Eurasian sources, the ancestral stocks arriving in waves over Indonesian archipelagic stepping stones. Those stocks that arrived first radiated farthest, such as the Australasian ratites, parrots, lyrebirds and honeyeaters; and those that came last changed least, such as the region's few Eurasian thrushes, pipits, larks, dicaeids. In Australia itself, the bird fauna of scleromorphic eucalypt vegetation was interpreted as the older and that of the rainforests as much younger, arriving from New Guinea in the Pleistocene.

Such a reconstruction fitted palaeogeographic and phylogenetic understanding of the times, that the earth's crustal blocks were fixed, that the morphological similarity between Eurasian and Australasian passerines reflected intra-familial connections, and that the subtropical Australian rainforests were Malesian in origin and recent in advent (Burbidge 1960). Despite the growing acceptance of continental drift over the last two decades, concessions to Gondwanan elements in the regional avifauna remained few.

Correlations among the diverse reviews presented today compel a different perception. There is now strong evidence of a massive endemic radiation in Australasian oscines, a radiation of such diversity that it must extend deep into the Tertiary. Consistent with this are the newly discovered fossils of oscines in inland Australia - among the oldest in the world - at a time when Australia had barely rifted from Antarctica and was still thousands of kilometers south of Eurasian island arcs. Their ancestral habitats, as exemplified in the parrots, were the subtropical rainforests that survive today in montane New Guinea and in pockets in coastal eastern Australia.

When integrated, these correlations suggest that the base elements of the autochthonous Australasian avifauna - its megapodes, parrots, halcyonine kingfishers, frogmouths and owlet-nightjars, and members of its Anseriformes, pigeons and particularly songbirds - as likely as not came from Gondwana. These elements dominate the Australasian land bird fauna today. The focus of its radiation was the stable Australian plate through the earlier Tertiary. Apart from their few surviving Gondwanan relicts, the avifaunas of New Zealand and New Caledonia have been built by overseas dispersal within the region. The core of the Australian land bird fauna developed in subtropical Gondwanan rainforest that covered much of Australia through the Tertiary



as Australia dessicated at its close, the rainforest avifauna withdrew to pockets on the east coast and newly-forming montane New Guinea, spawning scleromorphic vegetation-adapted elements in the process, in reverse to sequences postulated previously (Figure 1).

The only undisputable Eurasian immigrants are members of several near cosmopolitan waterbird and raptor genera, a handful of strigids, swifts and coraciids, and, in passerines, rarely more than one or two species in yet another handful of Eurasian-centred families: motacillids, laniids, turdids, dicæids, hirundinids etc. Together they comprise less than 20% of Australasia's modern land and freshwater avifauna.

This reconstruction has its own circumstantial difficulties, the most contentious of which is the assumption of a prevailing Gondwanan origin for the region's modern avifauna. As Boles (this symposium) stresses, elements of Gondwanan and Eurasian origin still cannot be distinguished with certainty. The issue is exemplified by the passerines. If they arose in Gondwana, as Olson (1989) and McLean (1990) postulate, were (1) Australasia's primary stocks of oscines inherited from Gondwana, from where they budded off dispersing stocks to Eurasia; or (2) did oscines first radiate in Africa, from where just one or two founders dispersed overseas very early to Australasia to establish the endemic Australasian radiation; or (3) were ancestral oscines split vicariantly into east (Australasian) and central (African) Gondwanan elements by the separation of Africa ca. 100 mya, spawning the radiation of holarctic oscines from African sources. Arguments can be mounted for and against all of these hypotheses; none resolve them.

Here the distinction of Gondwanan distribution from Gondwanan origin is crucial. Olson (1989) points out that a number of relictual, presumably Gondwanan groups in the southern hemisphere today also have a fossil record of late Cretaceous-early Tertiary age in the northern hemisphere. So too do the marsupials (Fox 1987). Even allied nondispersive genera of modern flowering plant families have such a bihemispheric distribution: *Fagus* and *Nothofagus*. Yet *Nothofagus* forest and the marsupials are classical examples of a relictual Gondwanan distribution today. Matching them are contemporary distributional connections among the casuariids, kiwis and tinamous (Bock & Buhler 1988), parrots, plains wanderers and seed snipe, magpie geese and screamers, and megapodes and cracids (Sibley & Ahlquist 1990). Whatever their origins, Australasian members of these groups surely came from Gondwana. Indeed, virtually all land bird elements present in Australasia up to the mid Tertiary 35 mya were eastern Gondwanan, because until that time Australasia was in touch with then-forested Antarctica, not Eurasia. As explanations, the diverse immigration tracks into Australasia – Eurasian, Antarctic, northern, southern, Malesian and Gondwanan – presently in vogue in Australian biogeographical literature (e.g. Rich 1975) are as misleading as they are redundant. Although Eurasian elements may have arrived via such routes, Gondwanan elements were inherited *in situ*. The concept of migration routes implies dispersal, confusing the difference between it and vicariance at continental level and the differing contributions that both processes have made to shaping the regional avifauna.

That Eurasian immigration of any substance did not begin until the later Tertiary, within the last 15-20 mya, is suggested as well by several ecological and palaeofloristic correlations in passerines. Those passerines of indisputable Eurasian

origin fall into two groups in Australasia. Either they are widespread members of Eurasian species that exploit niches unoccupied by autochthonous passerines (e.g. Long-tailed Shrike *Lanius schach*, and Pied Chat *Saxicola caprata*, in anthropogenic grassland in New Guinea, and Richard's Pipit *Anthus novaeseelandiae* of bare fields everywhere). Or they comprise small groups which have undergone endemic radiation to generic level in the regional grasslands and savannahs (e.g. estrildine finches, sylviid warblers).

Common to the habitats occupied by all of them is novelty and disturbance. Thus the savannahs and shrub steppes in which Australasian estrildines, sylviids and pipits are found are comparatively new to the region, their palaeogeographic record being no older than the late Tertiary when Australia began to desiccate (Barlow 1981). Correspondingly few autochthonous Australian passerines occur in these habitats, just as few Eurasian taxa have entered the endemic Australasian rainforests and scleromorphic vegetation. Here is historical evidence for the ecogeographical principle that the building of faunas by dispersal depends not just on ability to disperse but also the availability of niches and the ability to establish. It is a principle illustrated graphically in New Zealand today, in the contrast between the introduced European birdlife of its pastures and the indigenous avifauna of its native forests.

From an antipodean outpost, the Australasian avifauna has now moved towards the centre of the world's ornithogeographic stage. It holds historic clues and perhaps answers to such global questions as the relationships between continental avifaunas, the origin of the passerines, and the ecology of dispersal. In conclusion, however, a note of caution. Only a decade ago a completely different scenario for its origin and radiation was being espoused with equal conviction. Whether the perceptions advanced here today will stand in the future depends, quite simply, on continuing broad-based research into the phylogeography and palaeontology of the regional avifauna.

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SYMPOSIUM 3

**ORNITHOGEOGRAPHY
OF THE PACIFIC REGION**

Convener A. KEAST

SYMPOSIUM 3

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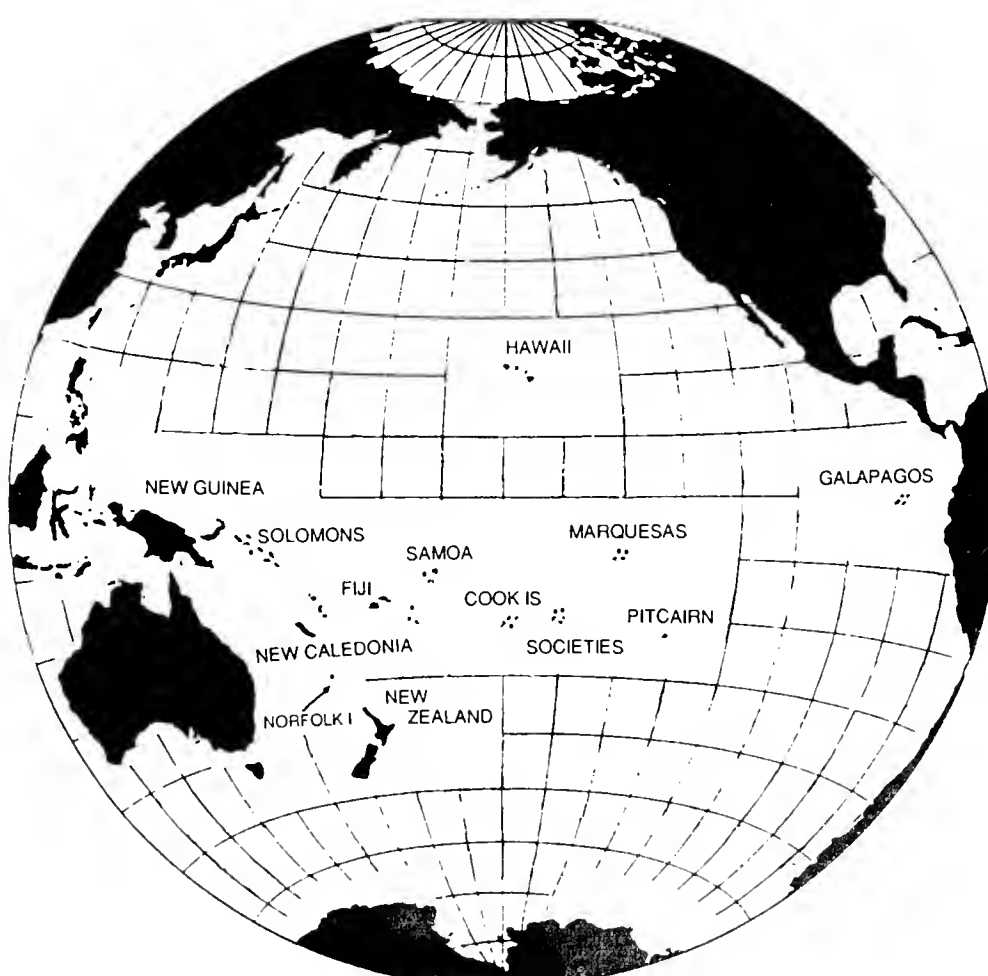
INTRODUCTORY REMARKS: ORNITHO GEOGRAPHY OF THE PACIFIC REGION

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The Pacific Region has figured importantly in biogeographic and evolutionary studies. Many major concepts of island evolution have been generated there. Hawaii contains the world's most exuberant and diversified archipelago fauna. The large island of New Guinea sports a degree of physical and biotic diversity approaching that of the best continental lowland rainforest and montane forest areas. New Zealand, an archaic continental relict, contains a mixture of old endemics and modern colonizers from Australia. The islands of the southwest Pacific show faunal attenuation and are active areas of insular speciation, as the studies of Mayr, and others, have demonstrated.

The objective of this symposium is to examine newer data relative to evolution in the Pacific Basin area. Of particular significance are the findings, from cave fossil data, that former avifaunas were distinct from modern ones. This necessitates a rethinking of basic concepts of Pacific ornithogeography. It is important to take another look at New Guinea now that more modern data on vertical and horizontal distribution, and on the ecology of major components, is available. It is appropriate to draw contrasts between the avifaunas of tropical New Guinea and cool temperate New Zealand, with its relatively small avifauna. Small insular avifaunas of the Pacific invite review in a community and ecological perspective.



THE CONTRIBUTION OF FOSSILS TO KNOWLEDGE OF HAWAIIAN BIRDS

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ABSTRACT. Fossils of Hawaiian birds reveal at least eight additional avian colonizations of the archipelago, and about 45 additional species of resident birds, thereby raising the number of species in the Holocene avifauna to about 92 and the number of avian colonizations to 20 or more. The colonizing species can be categorized as either waterbirds, raptors, or passerines. Flightlessness and terrestriality developed in over half of the waterbird lineages, adaptations for ornithophagy occur in half of the raptorial lineages, and adaptive radiation occurred in two out of five passerine lineages. The extinction of approximately 61 species of resident Hawaiian birds is attributed to the impact of human settlement of the islands.

Keywords: Hawaiian Islands, fossils, evolution, extinction, human impacts.

INTRODUCTION

Preliminary reports of rich avian fossil deposits in the Hawaiian Islands were published during the 1980's (Olson & James 1982a,b,1984, James 1987, James et al. 1987). Descriptions of seven new genera and 32 new species of birds represented in these fossil collections are in press (James & Olson in press, Olson & James in press), and three fossil genera and species were described earlier (Wetmore 1943, Olson & Wetmore 1976). Knowledge of the fossils has advanced enough to permit a reevaluation of evolutionary and zoogeographic trends in the resident, Holocene avifauna, taking into consideration both the fossil and historically known birds.

Besides the 35 extinct species referred to above, Hawaiian fossil collections include less diagnostic specimens that may represent up to 21 additional new species. A conservative estimate of the number of resident birds that became extinct before the historic period is 45 species, compared to 47 resident species that either still survive or became extinct during the historic period. Thus, there were originally at least 92 resident species in the Holocene avifauna of the main islands, 31 of which still survive, all but 10 of which are now thought to be threatened with extinction (Pyle 1988). These figures exclude species that probably did not colonize until after humans settled in the islands and created appropriate habitat for them (e.g., Black-crowned Night Heron, *Nycticorax nycticorax*^{*}, and Short-eared Owl, *Asio flammeus*).

The above figures also do not include an estimate of the number of extinct species for which fossils have not yet been found. Productive fossil deposits are known from only four of the eight main islands (Kauai, Oahu, Molokai, and Maui); a lesser amount of bone material is available from the island of Hawaii, mainly from archaeological

^{*}Taxonomy follows James & Olson (in press) and Olson & James (in press); common names follow Pyle (1988).

contexts; and little or nothing is available from the other islands. Thus, fossils have added 28 species to the avifauna of Maui, 24 to the avifauna of Oahu, 17 to the avifauna of Molokai, 11 to the avifauna of Kauai, four to the avifauna of Hawaii, one to the avifauna of Lanai, and none to the avifaunas of Kahoolawe or Niihau. More new species and distributional records can be expected as representative fossil collections become known from the poorly collected islands.

COLONIZATION

The historically known resident avifauna can be traced to 14 colonizing species (Mayr 1943), or, subtracting *N. nycticorax* and *A. flammeus* because they are probably post-human arrivals, to 12 natural colonizations of the main islands. Fossil evidence contributes at least eight additional colonizations, bringing the total to 20. This figure is a minimum, as it excludes two obscure fossil geese (*Geochen rhuax* and the Supernumerary Oahu Goose), and it incorporates the following assumptions: 1) the four species of flightless goose-like ducks (*Thambetochen* and relatives) are derived from a single colonization, 2) the flightless rails (*Porzana*) are derived from three colonizations, 3) the three species of Hawaiian crows are derived from one colonization, and 4) the two genera of Hawaiian honeyeaters (Meliphagidae: *Chaetoptila* and *Moho*) are derived from one colonization.

The 20 colonizers were an ibis (Plataleidae), two true geese (Anserinae), a dabbling duck (*Anas*), a second dabbling duck or a shelduck (Anatinae), three rails (*Porzana*), a gallinule (*Gallinula*), a coot (*Fulica*), a stilt (*Himantopus*), a hawk (*Buteo*), a sea eagle (*Haliaeetus*), a harrier (*Circus*), an owl (Strigidae), a crow (*Corvus*), a flycatcher (Myiagridae), a thrush (*Myadestes*), a honeyeater (Meliphagidae), and a finch (Carduelinae). The species that managed to colonize are divisible into three general categories: 11 were waterbirds, four were raptorial species, and five were passerines.

Continental relatives of many of the resident Hawaiian birds are recorded as occasional visitors in the islands (e.g., *Plegadis chihi* (White-faced Ibis), many species of *Anas* (dabbling ducks), *Branta canadensis* (Canada Goose), *Anser albifrons* (White-fronted Goose), *Haliaeetus pelagicus* (Steller Sea-Eagle), *Circus cyaneus* (Northern Harrier), and *Carduelis flammea* (Common Redpoll) (Pyle 1988). Although these species are not necessarily ancestral to related taxa in the resident fauna, their occasional arrival in the islands illustrates how colonization may have taken place.

The possibility also exists of colonization by island-hopping along the hot-spot islands of the Hawaiian-Emperor chain, most of which were submerged long ago and became seamounts (Jackson et al. 1972). This could result in the preservation of relictual taxa from as long ago as the late Cretaceous, the apparent age of the oldest seamount in the Emperor Chain (Scholl & Creager 1973, Worsley 1973). However, despite the growing fossil record there are still no obvious relicts in the Hawaiian avifauna, hence no evidence that avian lineages of extreme antiquity have been preserved by island-hopping from the older seamounts. Colonization of the main islands from the still subaerial Northwestern Hawaiian Islands has been proposed for the Hawaiian finches (Drepanidini) (Sibley & Ahlquist 1982).

EVOLUTION

Waterbirds

Eleven (55%) of the birds that colonized the main islands were waterbirds. An ecological shift from aquatic or semi-aquatic habitats to terrestrial habitats apparently occurred in seven of these lineages (*Apteribis*, *Branta*, a large goose from the island of Hawaii (Anserinae); *Thambetochen* and relatives, and the rails derived from all three colonizations by species of *Porzana*). Fossils of these birds are found in localities that are not near wetlands. Branching speciation, in which more than one endemic species has developed from a single colonization, occurred in at least 6 of the 7 terrestrial lineages, giving rise to 21 or 22 endemic species. Flightlessness is the rule among the terrestrial waterbirds, with all but one of the species in this group being completely (19-20 species) or nearly (one species) incapable of flying. Terrestrial waterbirds are the only group of Hawaiian endemics in which flightlessness evolved.

The four resident waterbirds that remained in aquatic habitats are *Anas wyvilliana* (Hawaiian Duck), *Fulica alai* (Hawaiian Coot), *Gallinula chloropus* (Common Moorhen), and *Himantopus knudseni* (Hawaiian Stilt). So far, no instances of flightlessness or branching speciation have been documented for these lineages, but there are few Holocene fossils of wetland birds.

Raptors

The Holocene fauna of the main islands includes seven raptorial species: *Haliaeetus* sp., *Buteo solitarius* (Hawaiian Hawk), *Circus* sp., and four strigid owls derived from a single colonization. The harrier and the four owls have long legs and short wings compared to related species outside the archipelago. Similar body proportions occur in bird-catching hawks of the genus *Accipiter*. Long-leggedness in Hawaiian raptors has been interpreted as an adaptation for hunting forest birds (Olson & James 1982b, in press).

Passerines

Fossils cast a new light on the spectacular adaptive radiation of the Drepanidini by adding 14 new species, descriptions of which are in press, and up to 8 additional undescribed species that are known from less diagnostic specimens (James & Olson in press). This raises the number of species in the radiation from 34, including three known historically from the Northwestern Hawaiian Islands, to between 48 and 56. Fossils also add to the diversity of the Hawaiian Corvidae and Meliphagidae, with two new species of crows and apparently two undescribed species of honeyeaters.

EXTINCTION

The approximately 45 Holocene extinctions recorded by fossils are attributed to the impact of prehistoric human settlement of the islands (Olson & James 1982a,b, 1984, James et al. 1987), which commenced about 1500 years ago (Kirch 1974). Human impacts during the historic period caused 16 additional extinctions of endemic species (Pyle 1988). The prehistoric and historic period extinctions should be viewed as one ongoing "extinction event", which so far has removed roughly as many species of birds from the Hawaiian Islands as there were mammals lost from North America at the end of the Pleistocene (see Anderson 1984 for a list of extinct Pleistocene mammals).

In the Hawaiian Islands, terrestrial waterbirds suffered almost universal extinction. All of the 19-20 flightless species are extinct, as is the one goose that was a weak flier at best. It is no coincidence that the sole surviving member of this group, *Branta sandvicensis*, is also the only species capable of sustained flight. Waterbirds that remained in wetland habitats fared better: these four species are still extant. However, the fact that no extinctions have been documented for wetland birds so far may be due to inadequate fossil sampling of wetland habitats.

All but one raptorial species (*Buteo solitarius*) suffered extinction. Contributing factors may have included low population numbers, disappearance of important prey species, and predation by humans. It is also possible that the raptors, like the flightless birds, were ground nesters. Ground nesters would be vulnerable to nest predation by rats, pigs, and dogs that were introduced by the Polynesians (Olson & James in press).

Among drepanidines, at least 12 (80%) of the species with finchlike bills were lost from the main islands, and 16 (50%) of the species with more derived bill shapes were lost, either during the historic or prehistoric periods. The relatively dry, lowland forests, which are now virtually absent from the islands, may have provided essential habitat for these birds.

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ECOLOGICAL IMPACT OF THE HUMAN DEPLETION OF FRUGIVOROUS BIRDS IN POLYNESIA

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ABSTRACT. The extinction and extirpation that accompanied the human colonization of Polynesia involved many obligate frugivores (pigeons, parrots) and partial frugivores (megapodes, flightless rails, certain passerines). On most islands, frugivorous species of the forest canopy have been reduced in number, while those of the forest understorey and floor have been eliminated. At first human contact, most islands in the Marquesas supported 2 or 3 rails, 6 pigeons and doves, 3 parrots, and a starling. Only 1 to 3 frugivorous species survive on the same islands today. Similar depletion occurred in the Society and Cook Islands. Even isolated Henderson Island has lost a ground-dove and two pigeons since Polynesians arrived 800 years ago. In Tonga, human impact has eliminated a megapode, 2 flightless rails, 5 pigeons and doves, 2 parrots, and a thrush on 'Eua. Similar losses must have occurred throughout the region. Because of the decline in frugivorous birds, particularly columbids capable of ingesting large fruits, some Polynesian forest trees may be unable to disperse naturally within or between islands today. This situation, now aggravated by mechanized forest clearing, may threaten survival of the forest trees.

BIOGEOGRAPHY OF NEW GUINEA BIRDS: A RE-EVALUATION IN LIGHT OF NEW SYSTEMATIC AND ECOLOGICAL INFORMATION

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ABSTRACT. New Guinea supports an enormous and biogeographically distinct assemblage of birds, one of the earth's four great tropical avifaunas. Past continental connections with Australia enabled the avifaunas of these two land masses to develop as a single one. As an equatorial mountainous island, New Guinea fosters the continued survival and evolution of the Australian rainforest avifauna, which, prior to the Pliocene, inhabited much greater areas on the now arid continent. Following the implications of current systematic and palaeontological studies, much greater endemism for the Australo-Papuan region is now recognized. Current evolution of new species in New Guinea follows two broad patterns. For montane birds, speciation appears to take place by isolation and differentiation of new forms along the Central Ranges. Diversity of lowland and hill forest species is centered on three broad coastal plains where rainfall reaches a maximum for the island. These areas probably served as refugia for lowland populations during arid periods of the Pliocene and Pleistocene. Research of this important avifauna lags far behind that of other tropical regions.

Keywords: Biogeography, avian palaeontology, speciation, New Guinea, Australia.

INTRODUCTION

Since the explorations of Alfred Russel Wallace (Wallace 1869), New Guinea has been known as the centre for an enormous and biogeographically distinct assemblage of birds, one of the earth's four great tropical avifaunas. Although only a tenth the size of Australia, the island of New Guinea supports a larger fauna of resident land and freshwater birds than its continental neighbour to the south. These totals currently stand at 578 species for New Guinea (Beehler and Finch 1985, Beehler et al. 1986) and ca. 535 for Australia (Keast 1981a). Geographically the two land masses seem so different: New Guinea, a densely forested island of swampy plains divided by a mountainous spine 2,000 km long and reaching altitudes of 5,000 m; Australia, an arid continent fringed with wooded hills. Yet, perched on the continental shelf of Australia, New Guinea is separated from its southern counterpart only by a shallow sea and political boundaries, which serve more as barriers to dispersal of ornithologists than of birds. Past continental connections with Australia have enabled the avifaunas of these two land masses to develop as a single one. Further, the combined tropical avifauna of Australia and New Guinea, the Australo-Papuan Region (Sclater 1858, Keast 1981a), has had a profound influence on the development of avifaunas of the Oriental region and of oceanic islands in the tropical Pacific. Despite the importance of the New Guinea avifauna, its significance to Australian ornithology is frequently forgotten. In part, this is because studies of New Guinea birds are few. For example, in this 20th IOC, the present paper is the only one of 140 symposia papers specifically addressing New Guinea birds. In this paper, I will review the biogeography of the New Guinea avifauna with emphasis on (1) development of the avifauna in relation to neighbouring regions and (2) abundant speciation on this now isolated island.

TABLE 1 – Distribution of selected families of land and freshwater birds breeding in the Australo-Papuan and Oriental Regions. Shown are numbers of genera and species breeding in Australia proper, New Guinea, Australia and New Guinea combined, “Oriental Region” including only peninsular SE Asia, and numbers of genera shared between the Australo-Papuan Region and Oriental Regions. Families of passerines are ordered artificially for comparison of ecological counterparts, between regions. Data from Beehler & Finch 1985, King et al. 1975 modified from Keast 1990).

Family	Australia proper	New Guinea	Australia & N.G.	Oriental & Aust/N.G. Oriental	
Anseranidae magpie goose	1-1	1-1	1-1	–	–
Dendrocygnidae					
whistling ducks	1-2	1-2	1-3	1	1-2
Anatidae ducks, geese	8-16	4-7	11-16	2	4-4
Megapodidae megapodes	3-3	3-7	5-9	–	–
Phasianidae					
pheasants, quail	1-3	2-3	2-4	1	20-39
Columbidae pigeons	11-21	14-44	19-58	7	9-30
Psittacidae parrots	20-52	21-45	33-88	1	3-9
Tytonidae barn owls	1-5	1-4	1-5	1	2-3
Strigidae typical owls	1-4	3-6	3-7	2	7-19
Podargidae*					
Austral frogmouths	1-3	1-2	1-3	–	–
Batrachostomidae*					
Asian frogmouths	–	–	–	–	1-5
Aegothelidae					
owlet-nightjars	1-1	1-6	1-6	–	–
Eurostopodidae*					
eared nightjars	1-2	1-2	1-4	1	1-2
Caprimulgidae* nightjars	1-1	1-1	1-1	1	1-4
Hemiprocnidae tree swifts	–	1-1	1-1	1	1-3
Apodidae swifts	1-1	2-6	2-7	2	5-10
Cerylidae*					
cerylid kingfishers	–	–	–	–	1-2
Alcedinidae*					
alcedinid kingfishers	1-2	2-4	2-4	2	2-6
Dacelonidae*					
dacelonid kingfishers	3-8	5-17	5-20	1	3-8
Meropidae bee-eaters	1-1	1-2	1-2	1	2-6
Coraciidae rollers	1-1	1-1	1-1	1	2-2
Bucerotidae hornbills	–	1-1	1-1	1	8-13
Certhiidae					
Northern treecreepers	–	–	–	–	1-4
Climaceridae					
Australian treecreepers	2-6	1-1	2-6	–	–
————— The old muscicapid assemblage —————					
Maluridae fairywrens	3-20	3-5	5-25	–	–
Acanthizidae					
Australian warblers	9-40	4-20	9-54	1	1-1
Eopsaltridae					
Australian robins	7-20	11-25	12-38	–	1-1
Orthonychidae logrunners	1-2	1-1	1-2	–	–
Pomatosomatidae					
Australian babblers	1-4	1-2	1-5	–	–

Cinclosomatidae whipbirds	2-8	4-6	5-14		
Monarchidae					
monarchs & magpie larks	5-14	5-20	5-22	—	3-4
Rhipiduridae fantails	1-4	1-12	1-12	1	1-5
Pachicephalidae whistlers	5-14	6-26	8-34	1	1-1
Muscicapidae	—	1-1	1-1	1	17-59
Turdidae	1-2	2-2	2-4	1	5-16
"Sylviidae" and "Timaliidae"					
Old World warblers					
& babblers	4-8	3-7	5-9	3	ca. 200

*familial arrangements proposed by Sibley & Ahlquist (1985)

WHY THE NEW GUINEA AVIFAUNA IS AUSTRALIAN—WALLACE’S SOLUTION TO A BIOGEOGRAPHIC PARADOX

Recognition of New Guinea’s role as principal refuge and source of tropical avifauna for Australia and Oceania dates back to initial exploration of the island by Wallace. Apparent at that time and since has been the striking discontinuity between faunal assemblages as one passes from Asia across the Malay Archipelago to New Guinea. Together with other vertebrate groups and insects, an Asian bird fauna gives way to an Australian one, in contrast to the vegetation which shows little change across the same gradient. Wallace noted that the discontinuity coincided with the geographic position of the islands: those islands on the Asian continental shelf supported an Asian fauna; landbridge islands off Australia supported an Australian fauna. Wallace hypothesized that seas had flooded the continental shelves, isolating the islands and their biotas.

For birds, the transition was especially evident among galliforms, most arboreal nonpasserine families and certain passerine families (Table 1). Groups that have radiated spectacularly in forests of New Guinea and Australia include pigeons, parrots, kingfishers, honeyeaters, birds of paradise, and bowerbirds. Cassowaries, megapodes, owlet-nightjars, and sittellas, though not so numerous, nevertheless are found only here. Up until ten years ago, other large groups of passerines were believed to be shared between Asia and Australia. Similar morphologies tied the austral warblers, flycatchers, thrushes, babblers, and others to the “muscapid assemblage” of Asia (Mayr and Amadon 1951) and supported the hypothesis that Australia derived much of its avifauna through waves of colonization by Asian immigrants. That these shared groups were passerine corroborated the idea that passerines worldwide had evolved and radiated recently (mid-Tertiary) relative to other bird families — another reason Australia would be principally at the receiving end of faunal interchange with Asia.

Avian systematic studies of the past decade brought about the dissolution of the muscapid assemblage (Mayr & Cottrell 1979, Sibley & Ahlquist 1985, Sibley et al. 1988) and further reshuffled other superficially similar passerine taxa in Australia and Asia, with the result that few of the large families are now considered shared between the two continental regions. Table 1 outlines the current taxonomic arrangement of the relevant passerines and nonpasserines, recognizing that relationships among these groups require further study.

Thus, a visit now to Wallace's realm finds an even greater division between the bird faunas of the Oriental and Australian Regions. The only large passerine families (>10 species in both region) with more or less equal representation in both regions are cuckoo-shrikes, starlings, orioles, white-eyes, and mannikins. Of these groups, the starlings, white-eyes, and mannikins clearly originated outside of Australia and, through their dispersal to much of the Pacific, colonized the island continent as well. All other large groups belong to one or the other continent with very thin representation across "Wallace's Line." Australian groups with a toe-hold on Asia include, at one species each, the Australian warblers, robins, logrunners (if you count *Eupetes*), whistlers, and woodswallows. Likewise, the family list for Australia is padded by Asian add-ons: bee-eaters, 2 species; rollers, 1; larks, 1; pipits, 2; sunbirds, 2; flowerpeckers, 2. Confusing the issue of endemism now is the family Corvidae as proposed by Sibley and Ahlquist (1985). Included in this assemblage besides the corvids proper are the cuckoo-shrikes, orioles, monarchs, fantails, drongos, cracticids, woodswallows, and birds of paradise; of these 9 closely related groups, 7 have their own history of exchange between Asia and Australia. Systematists who enjoy taxonomic and biogeographic tangles should pick at this one.

NEW GUINEA BIRDS AND PLATE TECTONICS

Wallace figured out that the land-bridge islands of the Oriental and Australian regions were just high ground on their respective continents and that rising oceans had cut them off. While this explained why the island biotas belonged to one continent or the other, broad differences between the biotas of the tropical Asian and Australo-Papuan regions remained unresolved until the advent of plate tectonics.

Debate over the origins of the Australo-Papuan avifauna has focused on two hypotheses: (1) successive colonization of birds from Asia followed by radiation of particularly successful groups and (2) development of entirely or largely endemic families on the continent itself, with the few founding lineages either having arrived very long ago or having been there since the origin of modern birds. Because of Australia's present isolation and the obvious recent arrival of certain Asian species, the colonization hypothesis was the first proposed (Mayr 1953, Darlington 1957).

Beginning in the late 1960s (Dietz & Holden 1969), the theory of plate tectonics provided an opportunity to consider the origins of the Australo-Papuan biota in a new historical context (Raven & Axelrod 1972, Keast 1981b). At the end of the Mesozoic, Australia was far south of its present position and, with Antarctica, formed a much larger continent. Seas separated this combined continent from South America and Africa, and some interchange of biota may still have been possible. Broadleaved evergreen forests predominated. Early in the Tertiary (53 million years ago), Australia split from Antarctica and moved northward, reaching its present position in the Miocene, approximately 10 million years ago. By this time, ice had spread over Antarctica obliterating the diverse terrestrial communities that must once have existed there and eliminating faunal exchange with South America and Africa. New Guinea's paleogeographic history began when island arcs formed in front of northward-moving Australia. Geological evidence (Löffler 1977, Douth 1972) confirms that these early islands were always situated on the Australian continental shelf and were not an independent land mass joined later. New Guinea never had the opportunity to evolve

a biota independently and has always been part of Australia (Schodde & Calaby 1972).

Recognition of the former proximity of Australia to Antarctica, South America, and Africa has invited the search for affinities among their avifaunas. Unfortunately the evolutionary and geological timetables discourage such an interpretation, for nearly all modern bird lineages did not appear until the Palaeocene or Eocene (Olson 1988). The great extinction event at the Cretaceous/Tertiary boundary that felled the dinosaurs and other elements of the Cretaceous fauna can hardly be expected to have spared the birds, though its effect cannot be evaluated as yet. Perhaps the number of bird taxa on each continent was much reduced. The quest for shared elements among the southern avifaunas (Cracraft 1976, Rich 1975a, b) have produced ambiguous results, the potential candidates from Australia and New Guinea being the emu and cassowaries (as ratites), waterfowl, megapodes, button-quails, pigeons, parrots, and owlet-nightjars, and other less likely groups. In the past, passerines were discounted as their lack of a fossil record before the Miocene suggested an ascendance long after the break-up of southern continents.

New interpretations of avian systematics (Mayr & Cottrell 1985, Sibley & Ahlquist 1985) have pushed back the age of passerines and suggest (1) that passerines are very old indeed, probably dating as far back as the presumed initial radiation of modern birds in the Paleocene and Eocene, and (2) that perhaps all groups of old Australo-Papuan passerines are derived from a single, endemic radiation. This interpretation puts passerines in the running as charter members of the avifauna shared among the southern continents (Feduccia & Olson 1982).

The most exciting evidence for origins of the Australo-Papuan avifauna comes from recent palaeontological work. Eocene sites in Europe and North America yielding large numbers of avian fossils, including associated skeletons, are currently being studied. Among the taxa identified are a number of modern groups formerly believed to be restricted to the southern hemisphere. Certain Australian taxa have turned up, including ratites, parrots, and owlet-nightjars. Olson (1988) has suggested that their modern distribution is relictual: these birds survived in Australia and died out elsewhere. Northern Eocene faunas differ also from modern ones in the taxa absent. The majority of ancient arboreal birds have been assigned to the Coraciiformes and Piciformes; none to the Passeriformes. Missing also are pigeons and, maybe, parrots. Among the waterbirds, the Anseriformes do not appear until the Miocene. As these groups are believed to date back this far, they may have originated in the Southern Hemisphere and spread to the north later. Unfortunately, contemporaneous sites have yet to be discovered in the southern continents. The oldest Australian bird fossils are of Miocene age. One wonders of the Australian Eocene: did the forests ring with the calls of coraciiforms and piciforms or the songs of passerines?

RELATIONSHIPS BETWEEN THE PAPUAN AND AUSTRALIAN AVIFAUNAS

In complete contrast to its present landscape of desert and woodland, Australia during the Tertiary supported vast tracts of mesic forest. This situation changed in the Pliocene as the continent became more arid. With the spread of xeric communities, rainforest persisted only in the eastern coastal ranges and, most importantly, in New

Guinea. The fossil record for plants and mammals documents the local extinction of rainforest biota across the continent (Schodde & Calaby 1972, Keast 1981b); for birds, a comparable record is being discovered (Boles 1991).

Unquestionably, the survival and continued evolution of Australia's tropical avifauna has depended almost entirely on the continued presence of rainforest in New Guinea. Australian endemic lineages centered in New Guinea include the cassowaries, megapodes, fruit-pigeons, lorries, pygmy and fig parrots, owlet-nightjars, dacelonid kingfishers, birds of paradise, berry-peckers, and longbills. Widespread Australian groups rich in Papuan genera and species include cuckoos, bowerbirds, robins, honeyeaters, acanthizid warblers, whistlers, monarchs, and others.

Australo-Papuan rainforest birds outside of New Guinea inhabit the long archipelago of forest patches that run down the east coast of Australia. The most species-rich patch, at the base of the Cape York Peninsula, supports only half the species diversity of equivalent forest in New Guinea. Many Australian rainforest bird species are shared with New Guinea and probably arose there.

Relationships between the tropical avifaunas of Australia proper and New Guinea have been studied extensively (Walker 1972, Schodde & Calaby 1972, Kikkawa et al. 1981). Differences between the avifaunas on either side of the Torres Strait can be accounted for by disproportionate extent of habitats rather than the present isolating effect of the Strait itself. For example, while the rainforest avifauna of Australia is impoverished in comparison to that of New Guinea, the woodland bird community of southern New Guinea supports only half the species of Cape York, even though the two communities constituted a single one less than 10,000 years ago when the Torres Strait did not exist and xeric woodland penetrated much further inland from the New Guinea coast. Many woodland birds of Cape York are presumed to have then inhabited New Guinea as well, and if so have since become extinct, as predicted by the model of MacArthur and Wilson (1967). Kikkawa et al. (1981), in a detailed analysis of the distribution of bird communities along the Cape York Peninsula, concluded that size and distribution of habitat patches determined bird distribution. A further process was a "filtering effect", a gradual attrition of rainforest species leading away from and woodland species towards New Guinea.

DISTRIBUTION AND SPECIATION WITHIN NEW GUINEA

Rainforests, by nature of their complex structure, moderate seasonality, and great diversity of food resources for birds, sustain far larger bird communities than other habitats. Relative to Australia proper, New Guinea maintains its diversity of tropical birds through (1) the immense expanse of its forests, which can support low-density bird populations large enough to escape extinction (MacArthur & Wilson 1967), (2) habitat diversity across gradients of moisture and altitude (Diamond 1972, Beehler 1982) and (3) extensive geographical regionalism (Diamond 1972, Pratt 1982).

Area effect

That larger areas hold more kinds of animals than smaller ones has been well documented. This certainly applies to birds in New Guinea, where, for example, larger mountain ranges hold more species than smaller ones. Most New Guinea birds live

in low population densities; in other words, they are rare. Any birder knows this who tries in a day to fill a species list of birds recorded from a particular area. Rareness is manifest not only in low numbers for widespread species. Patchy distributions, resulting presumably from local extinction, are characteristic of many uncommon species. The Banded Yellow Robin and White-rumped Robin are two examples of hill forest species recorded only from a dozen or so localities and then only at species-specific altitudes. Local, or complete, extinctions are poorly understood for continental avifaunas; however, large expanses of habitat appear to provide a buffer for reduced populations and to offer more opportunities for survival in hard times.

Altitudinal specificity

Structuring of avian communities in New Guinea is a complex topic and beyond the scope of this short review. However, one mechanism that deserves mention, because of its hypothesized role in speciation and development of the avifauna, is the distribution of birds along altitudinal gradients (Diamond 1972). As one passes from the coastal plain to the mountain summits, bird species characteristic of low elevations drop behind while closely related species of higher elevations take their place. Species turnover may happen more than once; as many as six species (e.g., robins) can be stacked along an elevational gradient. Because some species leave off without replacement, overall species richness declines. Each species characteristically specializes in an altitudinal band that remains fairly constant along the length of mountain range. While some species overlap broadly, others appear not to trespass apparent boundaries with neighbouring species.

Speciation and geographical regionalism

Local extinction and altitudinal segregation also bear on two broad patterns of regional endemism and speciation within New Guinea. For montane birds, the 2,000 km axis of the central ranges and 15 smaller outlying ranges provide ample opportunity for regional differentiation. Some ranges, such as the Vogelkop and Huon Peninsulas have accumulated a small assemblage of endemic species and a host of subspecies mixed in with the usual component of ubiquitous montane taxa (Diamond 1972, 1985). In addition, many species show patchy distributions; some being absent from seemingly suitable habitat. A proposed mechanism for speciation suggests that local extinction somewhere along the middle of a species' range is followed by differentiation of the two remaining separated populations. Upon reinvasion of the vacant middle ground, they again meet but do not interbreed because of newly acquired isolating behaviours. The two taxa now invade each other's range, but they split their altitudinal habitat, so that one passes below the other. Various stages of this scenario can be found among examples of New Guinea montane birds (e.g. White-throated Treecreeper, various *Parotia* species).

Principal centres of diversity for lowland birds occur in the south (Tran-Fly), west (Vogelkop) and North (Mamberamo/Idenburg). An analysis I conducted of geographical speciation for lowland birds proposes that regional differentiation of widespread forms takes place in these three refugia (Pratt 1982). Barriers for dispersal between the refugia are scarcely apparent today, for rainforest follows the coastal plain around the island. However, the dispersal corridors lie in regions of lesser rainfall (Paijmans 1976, McAlpine & Keig 1983). Scenarios for Pleistocene climatic regimes suggest that these channels literally dried up (Nix & Kalma 1972), becoming woodland or savanna, habitats totally unsuitable for most birds of lowland closed forest. This arid period also

transformed into woodland the outer coastal margins of the rainforest refugia. Upon return of more mesic conditions and expansion of rainforest the separated taxa met again. The few cases of sympatry also show that altitudinal specialization serves as a segregating mechanism. For example, in southern New Guinea the Brown-collared Brush-Turkey only occurs in hillforest while the Black-billed Brush-Turkey occupies the lowland plains; in northern New Guinea, where the former species occurs alone, it occupies both the lowlands and hill-forest.

CONCLUSIONS

If there is a single message to conclude this presentation, it is that Australia does not end at the Torres Strait. New Guinea holds the greater part of Australia's avifauna, and it also supports environments and taxa once far more widespread on the Australian mainland. Despite the diversity of New Guinea birds and their relevance to avian research in the Australasian region, ornithology of New Guinea lags far behind that of other tropical avifaunas. Great opportunities await researchers on this insular frontier.

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AVIAN EVOLUTION OF SOUTHERN PACIFIC ISLAND GROUPS: AN ECOLOGICAL PERSPECTIVE

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ABSTRACT. The west-east avifaunal attenuation from biologically rich New Guinea to the impoverished islands of the central Pacific embraces three zones: continental New Guinea, the Melanesian Arc islands (Solomons - Fiji, plus Samoa), and the isolated Polynesian (Pacific Plate) islands to the east. The pattern varies with level in the taxonomic hierarchy and taxonomic group. Groups differ in capacity to establish eastwards. Birds-of-prey, megapodes, and nectar-feeding meliphagids do not occur beyond Fiji-Samoa. Frugivores are widespread and make up a high proportion of the avifaunas of eastern Polynesia. Communities of the Melanesian islands, though numerically impoverished, are 'continental' in ecomorphological types present, division of feeding substrates, and feeding behaviours. Members of a community studied in the field (Taveuni, Fiji) did not have wider ecological niches or greater ecological overlap values than those of an 'equivalent' continental rainforest (Macpherson Range, Queensland). Central Pacific communities, by contrast, are depauperate and aberrant; some species show marked niche shifts. Newer geological data confirms that the Solomons, New Caledonia, and Fiji, the major centres of endemism, have occupied their present isolated positions through the Tertiary. Avifaunal origins by over-water dispersal, not vicariance, are confirmed.

Keywords: Avifaunas, bird distributions, communities, island evolution, Pacific biogeography.

INTRODUCTION

Although it has long been appreciated that the southwest Pacific region is one of the most interesting areas of avian speciation and evolution (e.g., Mayr 1931, 1934, 1940a,b, 1941, Galbraith 1956) the area has received only limited attention in later years (but see Diamond 1970, Diamond & Mayr 1976, Diamond & Marshall 1976). This paper provides an updated ornithogeography of that section from eastern New Guinea to the Marquesas, considering faunal attenuation and community structure in an ecological context.

METHODS

The review is based on the literature, measurements of museum skins, and field work in Tahiti (August, 1984), Taveuni, Fiji (January, 1982; October, 1990); Macpherson Ranges, Queensland (October, 1983; December, 1986; November, 1988). Feeding behaviour, use of feeding substrates, and foraging habits were quantified using a modified version of the methods of Holmes & Recher (1986), and Recher & Gebski (1990). Feeding events (prey attack counts) were limited to five per individual bird and 20-25 individuals monitored over periods of nine or more days. Ecological diversities and overlaps were calculated by the formula of Levins (1968) and Schoener (1970), respectively. For fuller details see Keast (1991), some results of which are incorporated here.

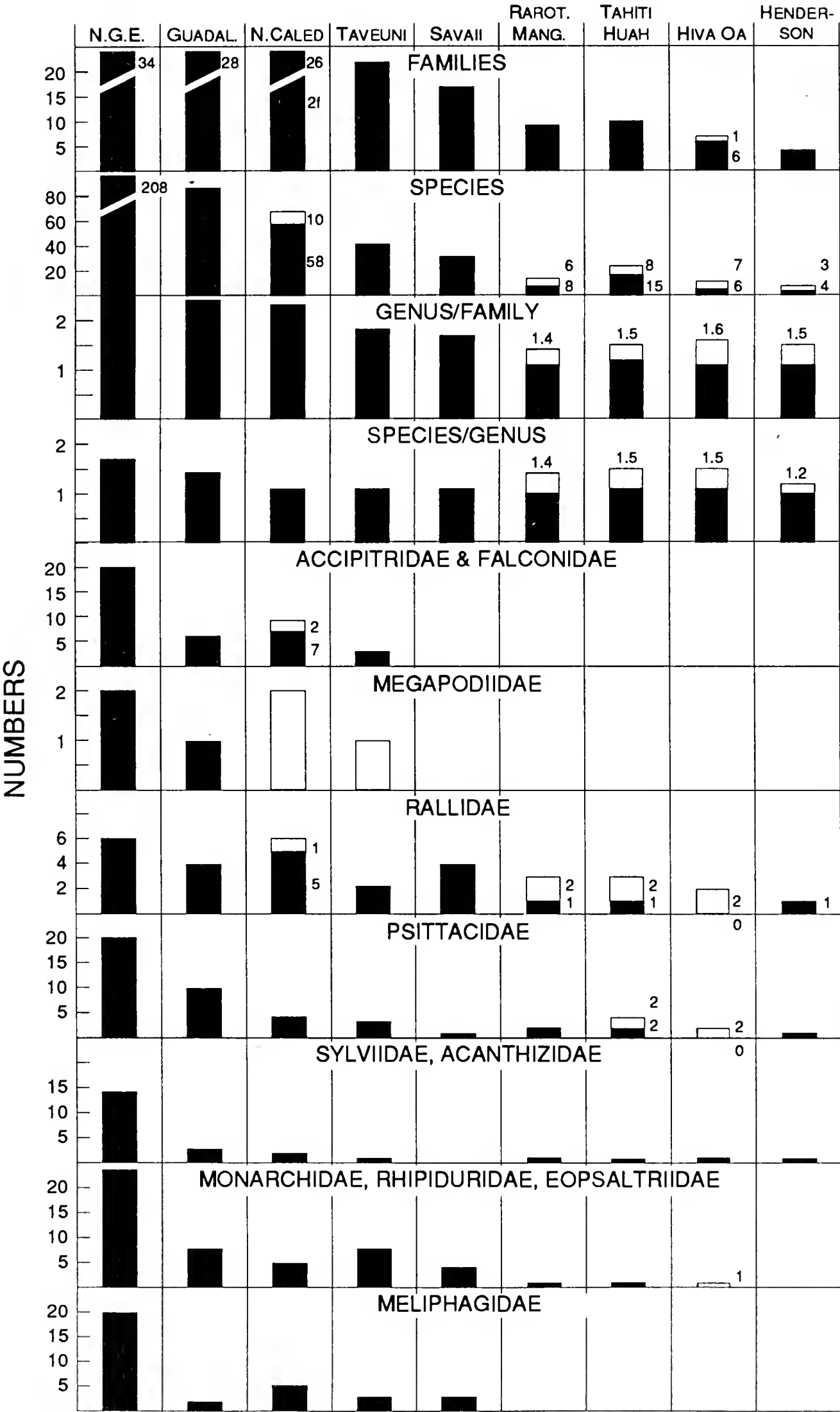


FIGURE 1 – Avifaunal attenuation, numerical representation of families, species, etc., and a subsample of avian families, eastern tip of New Guinea to Henderson Island. Additional fossil forms shown in white. New Caledonia has two extinct families, Hiva Oa one; Henderson, two *Ducula* pigeons (Steadman 1988, 1989). For degree of statistical difference between the Melanesian Arc and Pacific Plate avifaunas see Appendix 1.

The major islands

The major islands (see Figure in Introduction to the symposium) fall into three categories. New Guinea is large, continental, physiographically diversified and ornithologically very rich. Of modest size in the Oligocene most of it is of Pleistocene age. The Melanesian Arc islands (Solomons, New Caledonia, Fiji, New Hebrides) located towards the leading edge of the Australian Plate, are of intermediate size (e.g. Guadalcanal, 6,475 km²; New Caledonia, 16,750 km²); and also of mixed geological origin. All have been subaerial since the Miocene; New Caledonia possibly since the Cretaceous (Kroenke 1984). The Pacific Plate islands are small (Tahiti, 1,042 km², Hiva Oa and Rarotonga, 200 and 67 km²), volcanic, and have ages of 1-12 million years (Springer 1982). Their elevated areas (e.g. Tahiti reaches 2,238 m) are too restricted to support highland bird species. Inter-island distances between the major Arc islands are 800-1200 km; between the Plate islands, 1,200-2,100 km.

RESULTS

West-east avifaunal attenuation

Features of the major island avifaunas from west to east are shown in Figure 1. To eliminate the compounding effects of allopatry within archipelagos data is given only for major islands. Figures are adjusted to incorporate extinct forms (Steadman 1988). The following conclusions emerge:

(1) Drop-off in numbers of families is relatively uniform from New Guinea to Samoa, then falls precipitously. At the species level, by contrast, the drop occurs in three steps, between New Guinea and the Solomons, and east of Samoa. Genus/family ratios exceed 2.0 in New Guinea, Guadalcanal, and New Caledonia; are about 1.5 in Taveuni and Savaii; and 1.0 to the east. Species/genus ratios are 1.0 on all islands east of the Solomons, including New Caledonia, but are 1.2-1.6 for the plate islands if fossils are included. Statistical tests are in Appendix 1.

(2) The various avian groups differ markedly in eastwards distributions. Birds-of-paradise are confined to New Guinea; hawks, megapodes, meliphagids extend as far as Fiji/Samoa (Mayr 1978). Rails, parrots, pigeons, kingfishers, swifts, the warbler *Acrocephalus* and monarch flycatcher *Pomarea*, by contrast, occur throughout the central Pacific.

(3) Increasingly 'unbalanced' avifaunas result. Predators are absent east of Samoa. Frugivores (parrots, pigeons, starlings) make up an increasing percentage of the avifauna: vide eastern New Guinea, 40; Guadalcanal, 43; and for Rarotonga, Tahiti and Hiva oa (including fossil forms), 48-57. The reverse applies to insect-eaters. Varying ecological needs, as well as distance effects, presumably explain the differences.

Avian community structure, insectivores, Melanesian islands

Rain forest insectivore communities of Savaii and Taveuni at the eastern limits of Melanesia are compared numerically and in body sizes with 'equivalent' continental ones of the Macpherson Ranges, eastern Queensland, and Brown River, New Guinea (latter data from Bell (1982)) in Figure 2. Tarsus and bill lengths are plotted (scale, 10-40 mm). The former, of single measurements, is the best indicator of the bird's body size (Rising & Somers 1989). The latter reflects size of dominant prey being consumed (Hespenheide 1973). Both Tahitian species are large. Savaii and Taveuni, with fewer species, show the same body and bill size spreads as the continental communities.

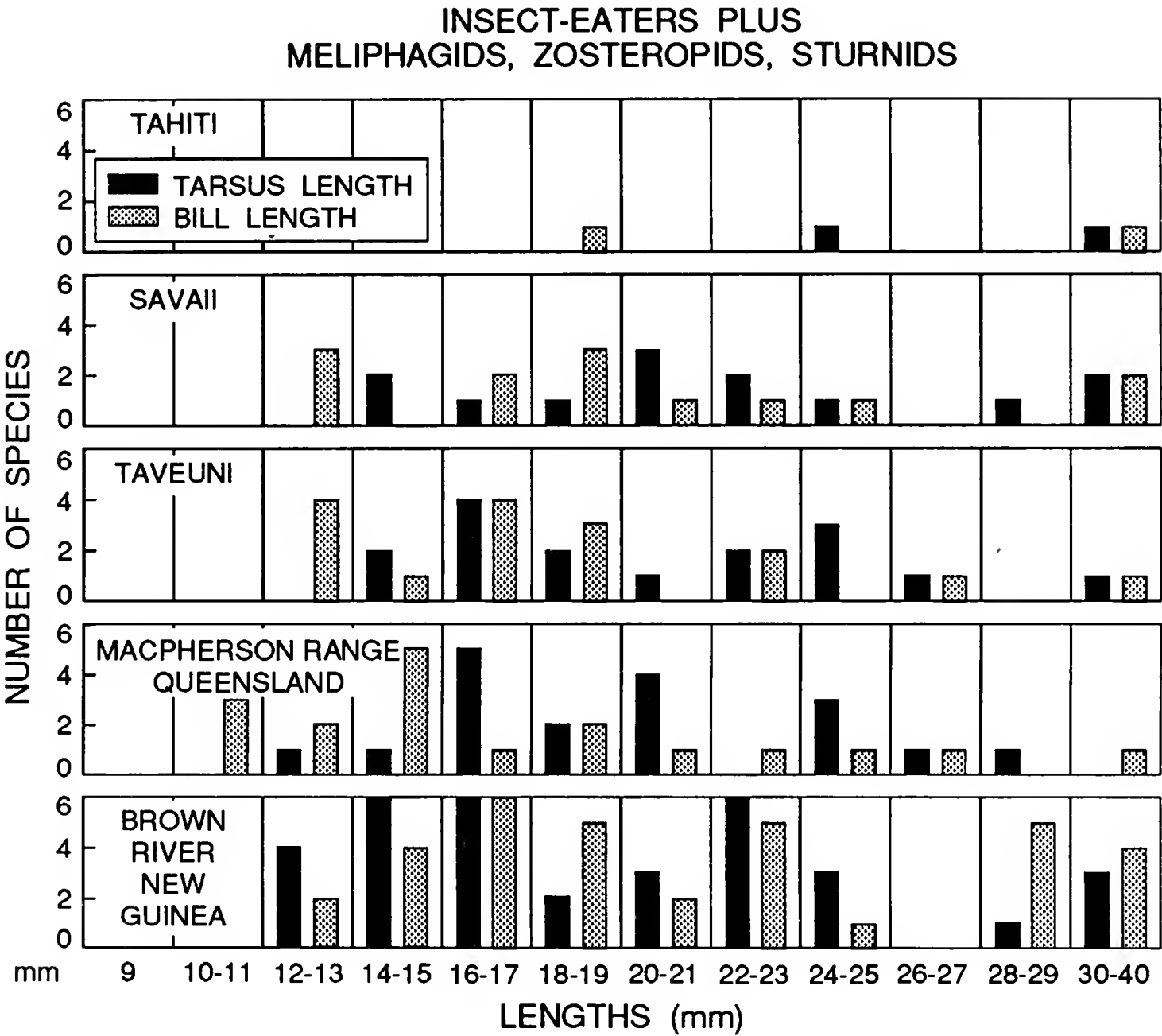


FIGURE 2 – Community structure of insect-eaters and part-insect-eaters, based on lengths of tarsus and bill: Tahiti (Society Islands), Savaii (Samoa), Taveuni (Fiji), Macpherson Range, southeastern Queensland, and Brown River, Papua. Melanesian Island Arc avifaunas have the same range of body size forms as continental ones, though species numbers are much smaller.

How does use of ‘ecological space’ compare? Taking Taveuni as the Melanesian island example, substrate use and foraging behaviours in six species are compared with six equivalent Macpherson Range forms (Figure 3). The Taveuni community separates into species that feed by gleaning from, and ‘fluttering at’, the foliage (*Mayronis lessonii*, *Petroica multicolor*, *Myiagra azureocapilla*); aerial feeder (*Rhipidura spilodera*, *Myiagra vanikorensis*); a trunk/branch and substratum feeder (*Lamprolia victoriae*); and an undergrowth-thicket feeder (*Vitia ruficapilla*). (The latter is not shown on the diagram.) These findings closely match those found by Holyoake (1979) for other seasons. It parallels the way feeding substrates are divided in the Macpherson Ranges community (Figure 3). How, then, are the greater number of species accommodated in the latter?. In part it is by a finer vertical partitioning of a feeding zone (Figure 3). That of the Taveuni *Rhipidura spilodera* is divided between *R. fuliginosa* and *R. rufifrons*, and *Petroica multicolor* between *P. rosea* and *Tregellasia capito*. In other cases two ecologically comparable species co-occur and are separated on microhabitat (e.g. *Acanthiza pusilla* and *Gerygone mouki*). For significance tests see Appendix 2.

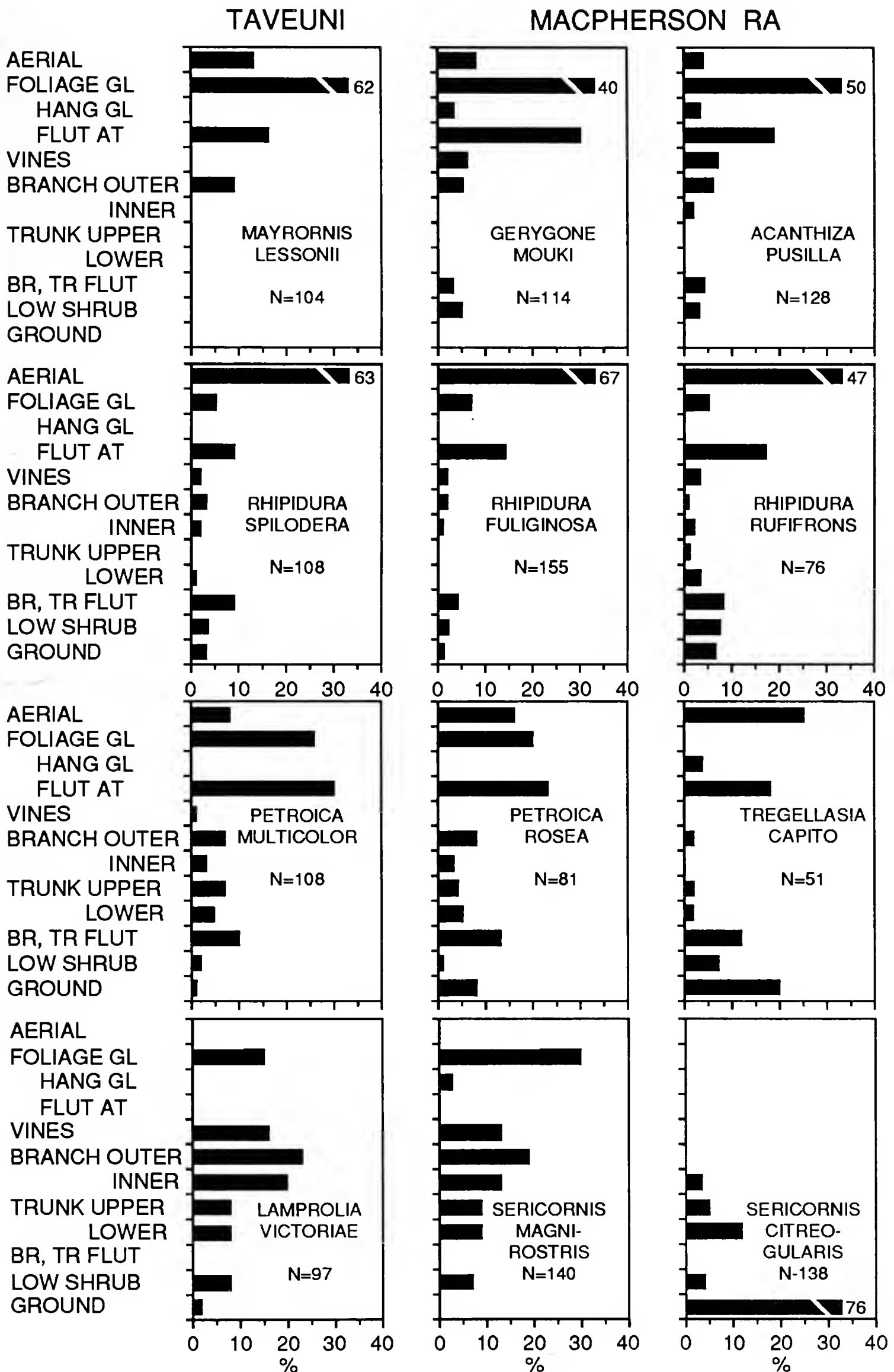


FIGURE 3 – Use of different substrates in foraging (numbers represent individual prey attacks), and foraging methods, six Taveuni and six Macpherson Range populations of species. For statistical treatment see Appendix 2.

How do members of the Taveuni insectivore bird community compare with the continental one in (a) degree of ecological diversity exhibited (feeding substrate utilization and prey attack manoeuvres) and, (b) in degree of niche overlap? Figures of these are given in Appendices 3 and 4. Average diversity figures for members of the Taveuni community (10 species) for substrate use are 3.09 and for the Macpherson community (12 species), 3.00. For prey attack behaviours they are 1.64 and 1.85. Average figures for ecological overlap for the Taveuni community (9 paired comparisons) are 0.53 for substrate use and for the Macphersons ones (11 comparisons) 0.36. For prey attack behaviours they are 0.63 and 0.67. The sets of figures are remarkably similar. The Taveuni community, hence, has a 'continental-type' structure in terms of these features, which presumably represent a stable state. Note, however, that niche shifts in island birds in the absence of competitors sometimes involves habitat changes (Diamond 1970).

Pacific Plate island communities

With their few species these communities contain striking examples of ecological shift and niche broadening. *Acrocephalus* is a short-billed reedbed and thicket insectivore in Asia and Australia. The long-billed insular derivatives of Polynesia, by contrast, consume a wide range of insect types, plus lizards, fruit and nectar (Holyoak & Thibault 1984). Kingfishers (*Halcyon*) are shoreline and ground-feeding forest forms in Australia. In Polynesia they are predominantly arboreal rain forest forms feeding on insects in the branches and foliage, and occasionally in the air; they also take crabs and hunt in streams. The flycatcher *Pomarea* apparently has a narrower niche, feeding largely in the foliage and not also the air (Holyoak & Thibault 1984). This means that there is no true forest aerial feeder. Swifts do not deviate from their typical role. *Acrocephalus* and *Pomarea* commonly separate on habitat, arguing that resources are limited (D. Holyoak, personal communication). Grant (1968), and others, have noted the frequency with which island insectivores have longer bills, possibly an adaptation for taking of a wider range of prey. The long bill of *Acrocephalus* could be regarded as an extreme example of this. 'Ecological release', expansion of the niche in the absence of competitors (Diamond 1970) could also be involved.

Centres of endemism and Pacific geological history

Endemic avian genera occur as follows: Solomons, 7; New Caledonia, 5; Fiji, 4; Samoa, 1 (Mayr 1978). Seven others occur on two or more island groups, indicating secondary spread. New Caledonia has an endemic family (Rhynochetidae), and a specialized fossil galliform (*Sylviornis*) of unknown affinities (Balouet & Olson 1989). Did these endemics arise by long distance dispersal, as the evidence suggests, or by vicariance (breakup of formerly continuous ranges)? Newer geological histories of the Pacific, incorporating plate tectonics (Coleman 1980, Kroenke 1984) show that whilst the Southwest Pacific has been highly dynamic tectonically the major island groups (Solomons, New Caledonia, Fiji) developed in their present position and have not, at least since the early Tertiary, been closer to each other and to the larger land masses than they are today. This confirms avian origins by over-water dispersal.

DISCUSSION

Diamond (1972) calculated the west-east attenuation rate for species from New Guinea into the central Pacific as representing a factor of two per 2,575 km. Earlier

Mayr (1940a,b) drew attention to the considerable avifaunal richness of the Melanesian islands compared to the impoverished Polynesian islands. This survey shows the picture to be more complicated. Attenuation patterns differ at the family, genus (Keast 1991), and species levels, in genus/family, and species/genus ratios, and according to taxonomic group. Whilst many ecological and taxonomic types are either confined to New Guinea, and/or the Melanesian islands, others extend to, and are highly successful in, the central Pacific. Parallel west-east attenuation patterns to those characterizing birds occur in many plant and animal groups. They are marked in mammals (Carter et al. 1946), reptiles, and many groups of plants and insects (listing in Thorne 1963).

What is the ecological meaning of decreasing species/genus ratios from west to east? This is to be expected because in any series such ratios decrease with decreasing species pool (Williams 1964). They may also indicate progressively reduced capacity to support closely related species (Grant 1966). Simberloff (1970) tested these alternative explanations for a large series of island groups. He found that deviations from predictions based on chance were not strongly correlated with island area, maximum elevation, and distance from the source. He concluded also that similarities between congeneric species may also be a factor limiting (or permitting) co-occurrence. See discussions of this subject in Peilou (1979, p. 225-226), and Brown and Gibson (1983, p. 526-527).

The avifaunas of the southwest and central Pacific have been exclusively developed from the west by long distance dispersal (Mayr 1940a,b). This has also been accepted for virtually all animal and plant groups. There is a considerable literature, some of it quite speculative, as to how various groups achieved their range patterns (Thorne 1963). The newer data on geological history of the Pacific cements the case for avian origins by dispersal rather than vicariance. Note, however, that Raven & Axelrod (1974) have argued that origin of the unique floras of New Caledonia and Fiji would require these lying close to Australia in the Cretaceous or Early Tertiary.

West/east attenuation patterns in the Pacific have presumably been built up over a long period of time and are now relatively stable. The occurrence of centres of endemism along the gradient do not change the basic pattern. Gradients are not unduly disrupted by differences in island sizes, or varying island distances. Large New Caledonia has an avifauna smaller than expectations. The Polynesian islands all have similar avifaunas despite their wide separations. Classic species/area effects do apply within the Solomons archipelago (Diamond & Mayr 1976), but not to the Polynesian island groups (Steadman 1988, 1989).

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APPENDIX 1

Numbers of families, genera, and species, are significantly different for a series of 12 Melanesian Arc islands relative to 7 Pacific Plate islands (that include those in Figure 1): Mann-Whitney test ($U = 84$; $P < 0.0001$ for extant forms; $U = 84$; $P < 0.0001$, if the Plate faunas are supplemented by extinct forms). Genus/family and species/genus ratios are significantly different between the two series for living forms ($U = 66$, $P = 0.04$; $U = 65$, $P = 0.05$). These ratios are marginally non-significant between the two series if extinct forms from the Plate islands are added ($U = 60$; $P = 0.13$; $u = 61$; $P = 0.11$).

APPENDIX 2

Statistical comparisons (χ^2) for division of feeding effort between substrates for four cases of Tavenui species seemingly being represented by two in the Macpherson Ranges (Figure 2) were made on the basis of one randomly chosen observation per individual (using random numbers table). Results are: *Mayrornis lessonii* and *Gerygone mouki* ($\chi^2 = 1.66$; $P = 0.8$); *M. lessonii* and *Acanthiza pusilla* ($\chi^2 = 3.33$; $P = 0.5$); *G. mouki* and *G. pusilla* ($\chi^2 = 2.2$; $P = 0.7$); *Rhipidura spilodera* and *R. fuliginosa* ($\chi^2 = 6.7$; $P = 0.5$); *R. spilodera* and *R. rufifrons* ($\chi^2 = 10.6$; $P = 0.2$); *R. fuliginosa* and *R. rufifrons* ($\chi^2 = 16.9$; $P = 0.02$); *Petroica multicolor* and *P. rosea* ($\chi^2 = 13.0$; $P = 0.07$); *P. multicolor* and *Tregellasia capito* ($\chi^2 = 42.8$; $P = 0.0001$); *P. rosea* and *T. capito* ($\chi^2 = 24.4$; $P = 0.001$); *Lamprolia victoriae* and *Sericornis magnirostris* ($\chi^2 = 3.7$; $P = 0.7$); *L. victoriae* and *S. citreogularis* ($\chi^2 = 30.6$; $P = 0.0001$); *S. magnirostris* and *S. citreogularis* ($\chi^2 = 141.6$; $P = 0.0001$). Thus *Rhipidura fuliginosa* and *R. rufifrons*; *Petroica rosea* and *Tregellasia capito*, and *S. magnirostris* and *S. citreogularis* (mainland species pairs); and *Petroica multicolor* (island) and *T. capito* (mainland), and *L. victoriae* (island) and *S. citreogularis* (mainland), are significantly different. On this basis only in one case (*Rhipidura*) does substrate use by the island form closely bridge the roles of two mainland species.

APPENDIX 3

Diversity indices, substrate utilisation and prey attack manoeuvres, formula of Levin's (1968).

Species	Substrate utilisation	Prey attack manoeuvres
(a) Tavenui		
<i>Petroica multicolor</i>	2.87	2.29
<i>Mayrornis lessonii</i>	1.58	1.83
<i>Pachycephala pectoralis</i>	2.41	1.11
<i>Myiagra vanikorensis</i>	3.26	2.89
<i>Myiagra azureocapilla</i>	2.40	1.81
<i>Rhipidura spilodera</i>	2.34	2.15
<i>Lalage maculosa</i>	2.12	1.06
<i>Vitia ruficapilla</i>	4.17	1.00
<i>Lamprolia victoriae</i>	5.95	1.00
<i>Zosterops explorator</i>	1.80	1.29
(b) MacPherson Ranges		
<i>Petroica rosea</i>	3.88	2.54
<i>Tregellasia capito</i>	4.89	2.82
<i>Pachycephala pectoralis</i>	2.78	2.46
<i>Rhipidura rufifrons</i>	3.51	2.76
<i>Rhipidura fuliginosa</i>	2.03	1.99
<i>Sericornis magnirostris</i>	5.53	1.00
<i>Sericornis citreogularis</i>	1.68	1.00
<i>Sericornis frontalis</i>	3.19	1.00
<i>Gerygone mouki</i>	1.73	2.22
<i>Acanthiza pusilla</i>	1.82	1.89
<i>Climacteris leucophaea</i>	3.64	1.00
<i>Zosterops lateralis</i>	1.70	1.51

APPENDIX 4

Ecological overlaps: substrate utilization and prey attack manoeuvres, Schoener (1970) index

Prey attack manoeuvres
(a) Taveuni

	<i>Petroica multicolor</i>	<i>Mayrornis lessonii</i>	<i>Pachycephala pectoralis</i>	<i>Myiagra vanikorensis</i>	<i>Myiagra azureocapilla</i>	<i>Rhipidura spilodera</i>	<i>Lalage maculosa</i>	<i>Vitia ruficapilla</i>	<i>Lamprolia victoriae</i>	<i>Zosterops explorator</i>
<i>Petroica multicolor</i>	-	0.76	0.57	0.65	0.86	0.45	0.55	0.52	0.52	0.56
<i>Mayrornis lessonii</i>	0.73	-	0.76	0.55	0.82	0.48	0.74	0.71	0.71	0.71
<i>Pachycephala pectoralis</i>	0.83	0.97	-	0.31	0.71	0.24	0.95	0.95	0.95	0.87
<i>Myiagra vanikorensis</i>	0.59	0.54	0.51	-	0.58	0.79	0.29	0.26	0.26	0.26
<i>Myiagra azureocapilla</i>	0.79	0.72	0.89	0.54	-	0.37	0.66	0.61	0.61	0.66
<i>Rhipidura spilodera</i>	0.41	0.34	0.30	0.73	0.28	-	0.22	0.19	0.19	0.19
<i>Lalage maculosa</i>	0.77	0.76	0.85	0.57	0.90	0.29	-	0.97	0.97	0.87
<i>Vitia ruficapilla</i>	0.59	0.33	0.42	0.41	0.45	0.39	0.37	-	1.00	0.87
<i>Lamprolia victoriae</i>	0.51	0.25	0.56	0.42	0.57	0.34	0.49	0.67	-	0.87
<i>Zosterops explorator</i>	0.64	0.67	0.69	0.43	0.74	0.22	0.74	0.44	0.48	-

APPENDIX 4 – continued

(b) Macpherson Range

	<i>Petroica rosea</i>	<i>Tregellasia capito</i>	<i>Gerygone mouki</i>	<i>Acanthiza pusilla</i>	<i>Sericornis magnirostris</i>	<i>S. frontalis</i>	<i>S. citreogularis</i>	<i>Pachycephala pectoralis</i>	<i>Rhipidura fuliginosa</i>	<i>R. rufifrons</i>	<i>Zosterops lateralis</i>	<i>Climacteris leucophaea</i>
<i>Petroica rosea</i>	-	0.89	0.86	0.75	0.48	0.48	0.48	0.98	0.47	0.67	0.54	0.48
<i>Tregellasia capito</i>	0.70	-	0.82	0.72	0.45	0.45	0.45	0.87	0.58	0.78	0.51	0.45
<i>Gerygone mouki</i>	0.59	0.48	-	0.90	0.78	0.78	0.78	0.86	0.41	0.61	0.69	0.78
<i>Acanthiza pusilla</i>	0.62	0.44	0.93	-	0.69	0.69	0.69	0.76	0.38	0.55	0.79	0.69
<i>Sericornis magnirostris</i>	0.62	0.55	0.47	0.51	-	1.00	1.00	0.49	0.15	0.28	0.80	1.00
<i>Sericornis frontalis</i>	0.30	0.43	0.10	0.09	0.30	-	1.00	0.49	0.15	0.28	0.80	1.00
<i>Sericornis citreogularis</i>	0.26	0.35	0.05	0.06	0.21	0.65	-	0.49	0.15	0.28	0.80	1.00
<i>Pachycephala pectoralis</i>	0.81	0.59	0.78	0.81	0.58	0.17	0.13	-	0.45	0.65	0.55	0.49
<i>Rhipidura fuliginosa</i>	0.43	0.53	0.38	0.37	0.33	0.09	0.06	0.45	-	0.80	0.21	0.15
<i>Rhipidura rufifrons</i>	0.57	0.71	0.42	0.40	0.47	0.27	0.21	0.51	0.79	-	0.34	0.28
<i>Zosterops lateralis</i>	0.51	0.41	0.83	0.59	0.42	0.27	0.07	0.66	0.28	0.35	-	0.80
<i>Climacteris leucophaea</i>	0.33	0.13	0.06	0.12	0.50	0.23	0.10	0.22	0.08	0.15	0.05	-

SYMPOSIUM 4

**SYSTEMATICS AND BIOGEOGRAPHY
OF AFROTROPICAL BIRDS**

Conveners T. M. CROWE and C. H. FRY

SYMPOSIUM 4

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INTRODUCTORY REMARKS: SYSTEMATICS AND BIOGEOGRAPHY OF AFROTROPICAL BIRDS

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Africa has a very special place in the history of mankind. If the mounting palaeontological and biochemical evidence is correct this splendid continent was the evolutionary cradle for both the genus *Homo* and for modern humans. Yet, *Homo sapiens*, man the wise, is in the process of destroying much of the fabulous biota to which his own future is inextricably linked. Even the most optimistic conservation scenarios for Africa predict that a large number of species are already doomed to extinction. There will be just too little room in the ever shrinking ark. Thus, like it or not, man the wise, or perhaps more appropriately, man the inconsiderate and short-sighted 'wise guy', will soon have to make some very tough decisions as to which taxa and populations should be saved. It is up to us as systematic biologists and biogeographers to provide the evidence necessary to help make correct decisions in this terrible triage. Providing decision-makers with species inventories is not enough. At higher taxonomic levels, we need to identify the major evolutionary lineages that need to be preserved to maximise evolutionary potential. At the lowest taxonomic levels, we need to know what patterns of within-species variation are needed to preserve a species' genetic integrity and thus ensure its long-term survival. From a biogeographical perspective, how many reserves will be needed and how large and far apart must they be to preserve the surviving biota.

I believe that the papers presented at this symposium will be valuable contributions in this regard. However, before I ask the first speaker to begin, I would like you to please stand up and join me in a brief moment of silence to protest the ill-conceived, ill-considered and ill-advised decision of the executive of the British Natural History Museum to abolish ALL of the research-oriented posts in its Sub-department of Ornithology and charge visiting scientists substantial daily 'bench fees'.

TRENDS IN THE LITERATURE OF AFROTROPICAL ORNITHOLOGY

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ABSTRACT. 13,662 citations in the *Zoological Record* from 1864 to 1980 inclusive which deal wholly or substantially with the birds of the Afrotropical Region (but not Madagascar) were identified and analyzed for various aspects. The predominance of citations dealing with taxonomy in the first 90 years was not maintained. A rise in the number of citations dealing with studies of living birds began in the 1950s and has been maintained since then. Biogeography was studied chiefly in the two decades 1951-1970 and systematics chiefly in the two decades 1941-1960. The Falconiformes and Charadriiformes (among others) were understudied before the 1950s, but this has since been more than remedied. There has been a recent decrease of interest in the Caprimulgiformes and Piciformes. The Passeriformes has never attracted as much attention as the number of its species warrants. This is a worldwide phenomenon.

Keywords: Afrotropical ornithology, history, taxonomy, distribution, Caprimulgiformes, Charadriiformes, Falconiformes, Galliformes, Passeriformes, Piciformes, Procellariiformes.

INTRODUCTION

This paper is a contribution to a full history of ornithology in the Afrotropical Region, a work that has yet to be undertaken. Here we report on trends in topics of ornithological study, based on the Afrotropical literature as recorded in the *Zoological Record Aves* from 1864 to 1980. There has been no detailed study or analysis of the whole contents of the *Zoological Record*. However, aspects have been noted by Besterman (1966 cited by Bridson 1968), Dadd (1971) and Chisman (1990). Only Besterman (1966) alluded even briefly to birds.

Before the *Zoological Record* was established by Alfred Günther, there were earlier attempts to list or catalogue zoological publications, the most important of which was A.F.A. Wiegmann's *Archiv für Naturgeschichte* from 1835 to 1914 which included birds, but not one of them was as complete as the *Zoological Record* (Bridson 1968). This is still true (Chisman 1990). As far as Afrotropical ornithology is concerned, the most comprehensive listing of its literature for the 19th century is the 43 pages in Reichenow (1900). The next most important listing is the 71 pages in Chapin (1954).

METHODS

Each year's *Zoological Record Aves* was scanned for citations dealing with Afrotropical birds, and the geographical breakdown provided therein was examined to check that all citations had been found. Each citation was given a unique identifying number. Since most of the literature is based on political entities or subdivisions thereof, the Afrotropical Region (chiefly Africa south of the Sahara Desert) was taken to include the whole of Mauritania, Mali, Niger, Chad and Sudan. Southwestern Arabia and oceanic islands, of which the largest is Madagascar, commonly regarded as Afrotropical, were excluded.

Citations (separate entries, usually numbered, in the author index of each issue of the *Zoological Record*) were regarded as Afrotropical if it appeared from their titles or the geographical breakdown provided in the *Zoological Record* that they dealt entirely or substantially with Afrotropical birds within the region or in zoos, aviaries or laboratories elsewhere. Physical examination of citations was not normally attempted owing to time constraints and, with some of the 19th century literature, because it is not readily available.

Identified citations were coded for computer analysis. Aspects coded included year of publication, principal topic of the citation (its main theme or purpose), important subsidiary topics of the citation where present, and the Wetmore (1960) order of birds covered when only one avian order was involved. Wetmore's system was used because it is the best known, not because we endorse it *vis a vis* other systems. All categories used are mutually exclusive in both statistical and logical senses, but the 38 topics defined in Appendix 1 are mutually exclusive only in the statistical sense.

Citations were grouped into decades, e.g. 1891-1900, for analysis and detection of trends. Chi-square or, alternatively, log-likelihood ratio tests of independence for contingency data were undertaken, using SAS statistical software where appropriate (SAS User's Guide 1985); the null hypothesis tested for each aspect being no change in relative citation frequencies between 1864 and 1980 inclusive. The null hypothesis for each aspect was rejected at the 5% significance level.

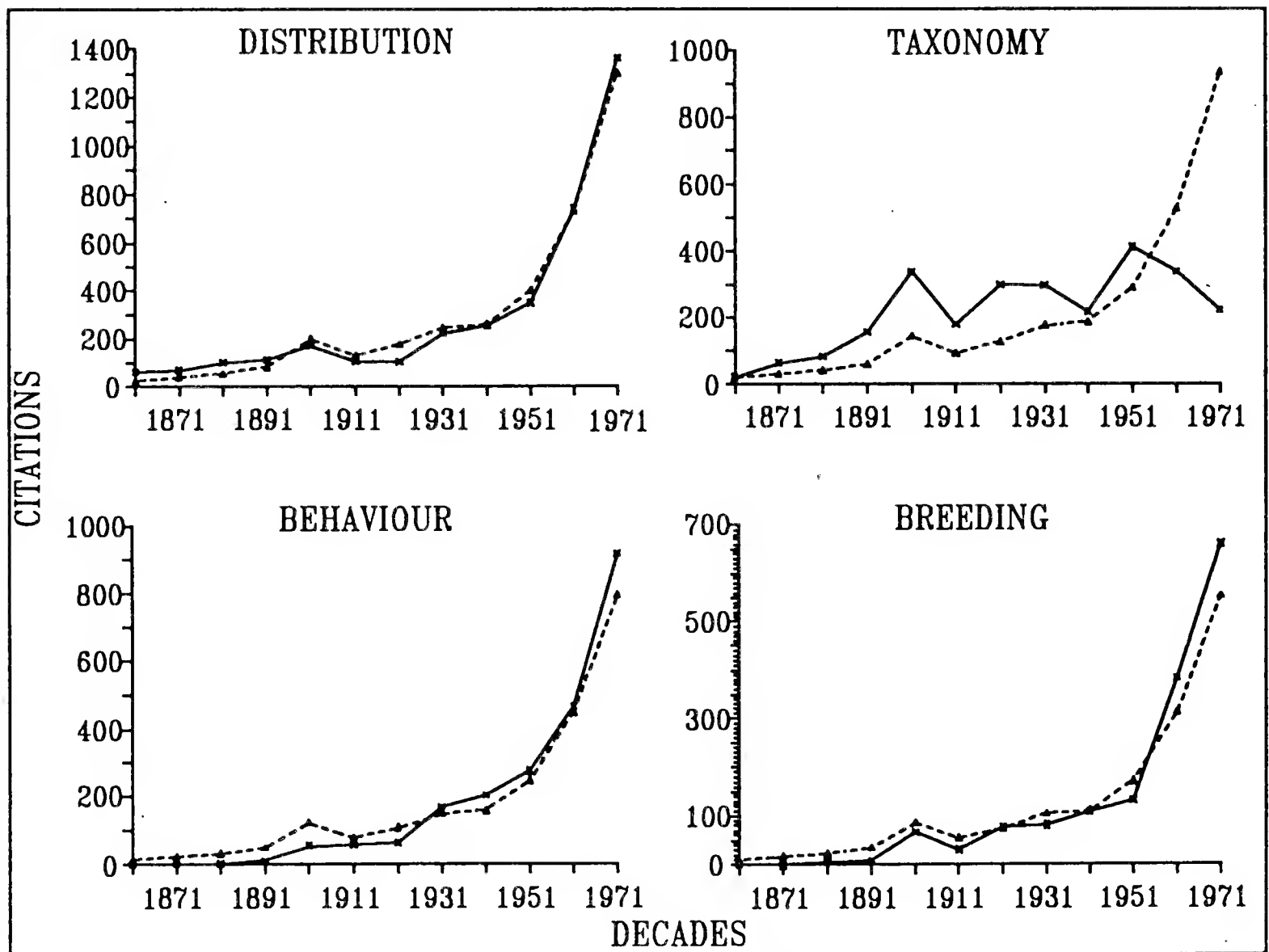


FIGURE 1 - The relationship between actual (solid line) and expected (dashed line) numbers of citations for the four most studied principal topics (defined in Appendix 1) by decades.

RESULTS

13,662 citations were identified and analyzed. The main results concerning taxonomy/systematics, distribution/biogeography and attention shown to different orders are given below.

Principal topics

The most frequent principal topics of study (the main theme or purpose of a citation) have been distribution, taxonomy, behaviour and breeding, in descending order of frequency (Figure 1). Each of these topics has frequencies an order of magnitude greater than the next most investigated topic, diet. However, only in the 1800s and in the decades after 1960 were there more distribution papers than expected. Breeding only became prominent in the 1960s, whereas behaviour became prominent in the 1930s. Taxonomy was the leading principal topic between the last decade of the 1800s and the 1950s, as the small piciforms and passerines were extensively sampled. The relative number of taxonomic papers decreased markedly in the 1960s, and taxonomy has not regained its status as the leading principal topic since then.

Biogeography, for which there are only 108 citations, was most often studied between 1941 and 1980, although it was only in the 1950s and 60s that the number of citations exceeded expectation. Systematics, for which there are only 81 citations, was most often studied between 1941 and 1980, although it was only in the 1940s and 50s that the number of citations exceeded expectation.

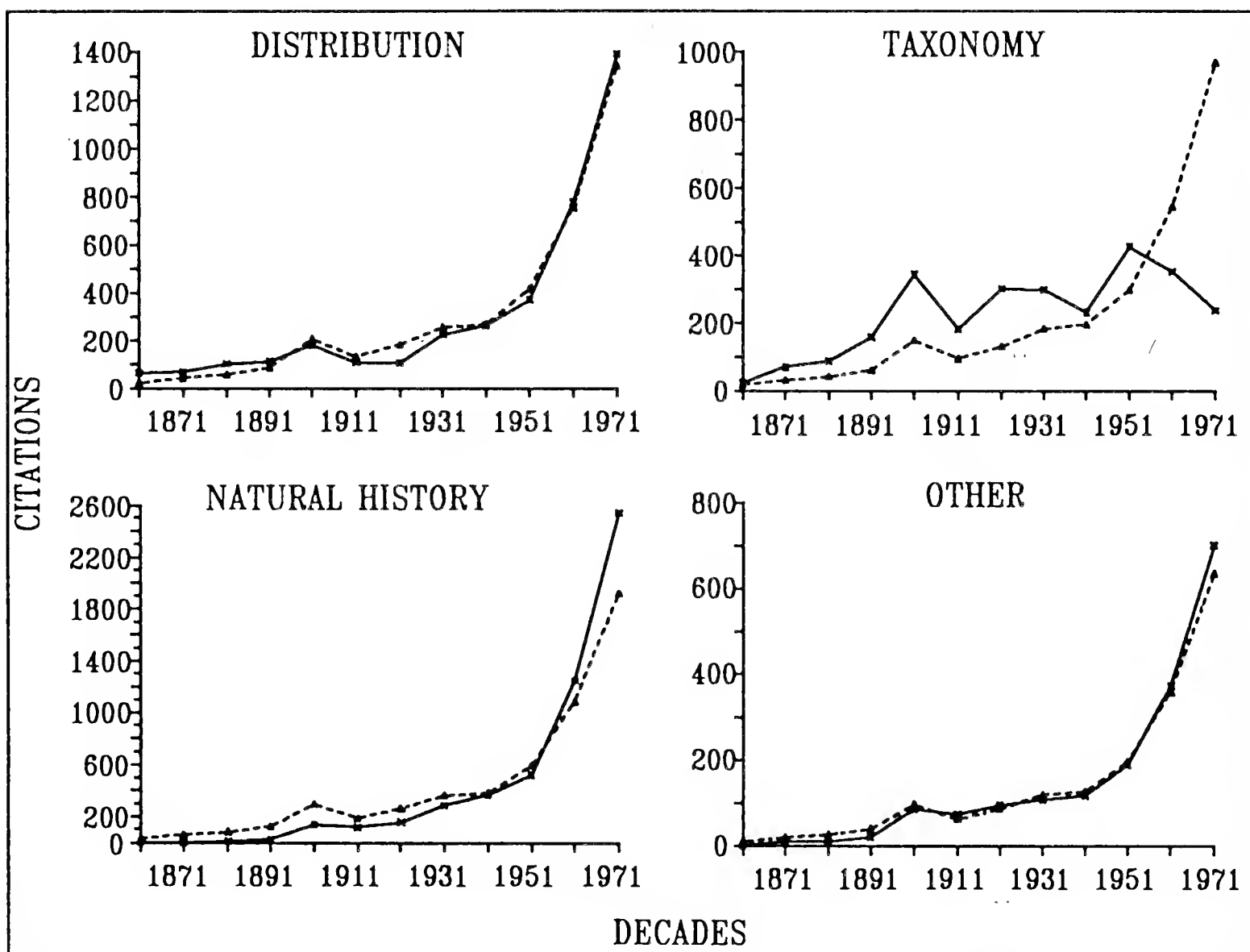


FIGURE 2 - The relationship between actual (solid line) and expected (dashed line) numbers of citations for topics grouped into four major themes by decades.

Figure 2 shows the results of amalgamating the 38 principal topics into four: taxonomy (including systematics), distribution (including biogeography), natural history and all topics not previously specified. Changes in the attention given to taxonomy and distribution have been noted in the preceding paragraph. Natural history did not even approach its expected number of citations until the 1940s, and it was only from the 1960s onwards that its citations exceeded expectation, i.e. when taxonomy fell below it. All topics not previously specified are too heterogeneous for comment.

Subsidiary topics

The four most important subsidiary topics (major elements of a citation which are not its main theme or purpose) are the same as the four most important principal topics (Figure 3). The pattern between these four subsidiary topics broadly complements that of the principal topics. Behaviour is the most important in terms of citations, but only became prominent around the beginning of the 20th century as, prior to that, workers usually concentrated on taxonomy and distribution. Taxonomy is the second most prominent subsidiary topic, followed by breeding and distribution. Taxonomy and distribution are highly correlated as topics, occurring together in many citations: hence the inversion of importance between these two topics from that found in studying the principal topics. Taxonomy was the most frequent subsidiary topic in the 1800s, but decreased markedly in the 1910s. Distribution was at its height as a subsidiary topic between 1921 and 1959, then decreased, which taxonomy did as a principal topic.

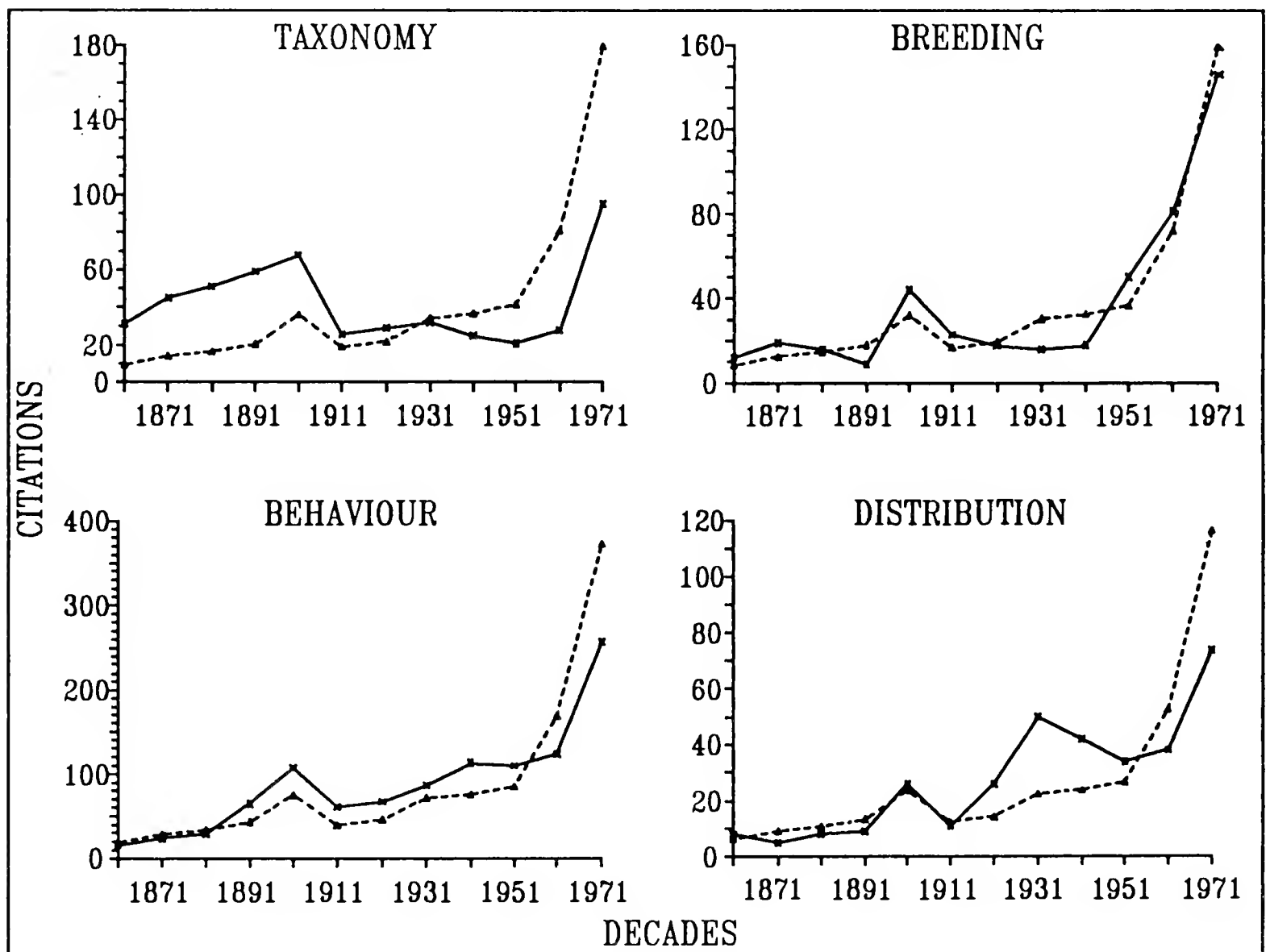


FIGURE 3 - The relationship between actual (solid line) and expected (dashed line) numbers of citations for the four most studied subsidiary topics (defined in Appendix 1) by decades.

The number of citations dealing with breeding as a subsidiary topic generally parallel the expected number, never reaching any great height.

Orders

The null hypothesis that members of orders were written about in proportion to their numbers in the Afrotropical avifauna (1,965 species, including vagrants) proves to be substantially true for six orders, viz. Podicipediformes, Gruiformes, Columbiformes, Strigiformes, Trogoniformes and Coraciiformes. The Struthioniformes and Galliformes have always attracted disproportionately great attention, whereas disproportionately little attention has been given to the Procellariiformes and Passeriformes (Figure 4; Table 1). Nine orders (Sphenisciformes, Pelecaniformes, Ciconiiformes Anseriformes, Falconiformes, Charadriiformes, Psittaciformes, Apodiformes and Coliiformes) have moved from expectation or below it to above expectation at one time or another in the 20th century. Three orders (Cuculiformes, Caprimulgiformes and Piciformes) have recently moved from expectation or above it to below expectation.

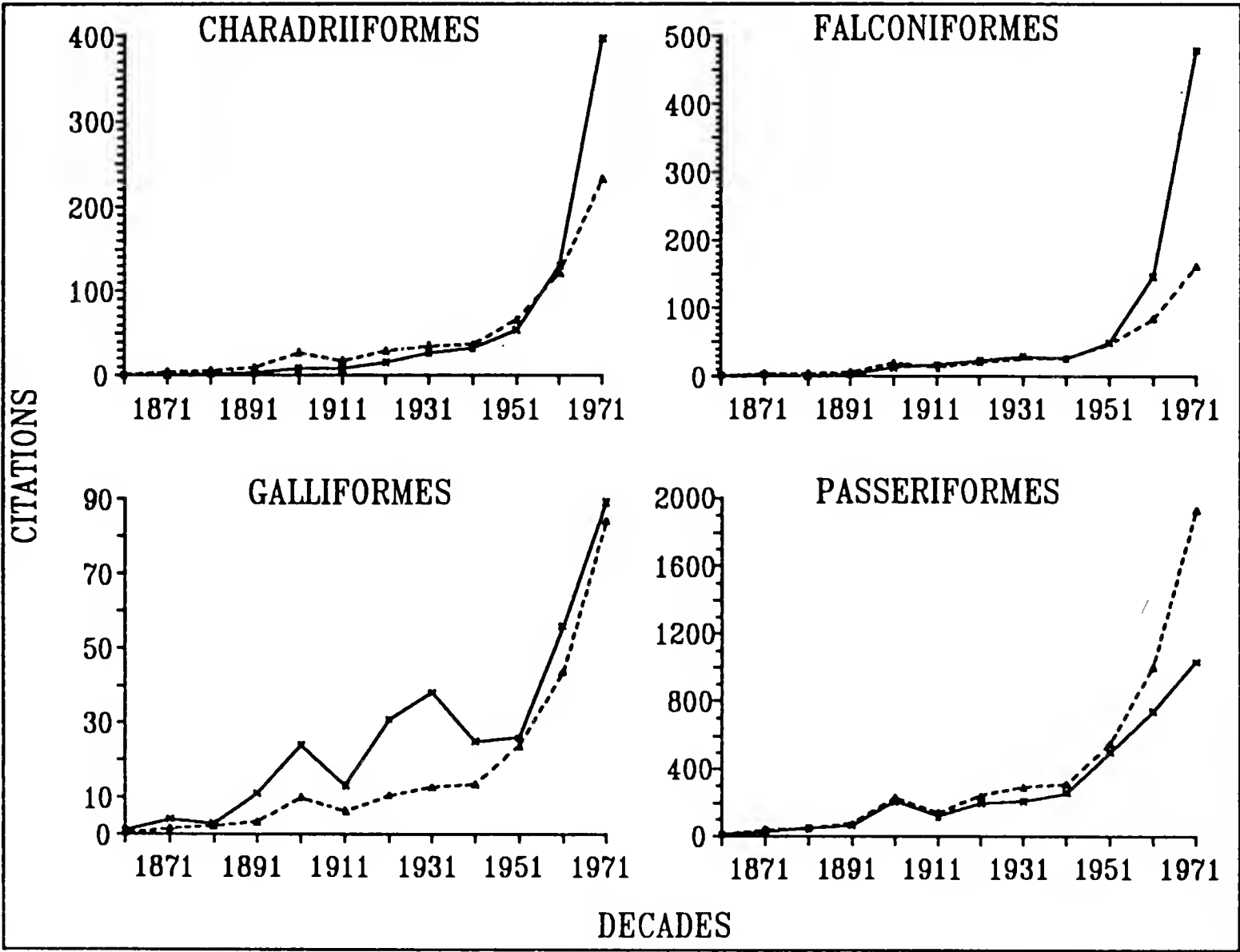


FIGURE 4 - The relationship between actual (solid line) and expected (dashed line) numbers of citations referring to four orders by decades.

TABLE 1 - Percentage of worldwide citations in *Wildlife Review* dealing with passerines as opposed to other orders: Passeriformes constitute 58.4% of all bird species (Morony et al. 1975).

Year	Percentage of passerine citations	Year	Percentage of passerine citations
1976	29.5	1983	30.6
1977	26.4	1984	31.3
1978	31.1	1985	28.5
1979	30.7	1986	26.6
1980	30.2	1987	27.4
1981	31.5	1988	28.2
1982	31.1	1989	30.0

DISCUSSION

The *Zoological Record* provides an operational baseline for studies such as this, even though it is known to be incomplete and to contain errors, not to mention changes in editorial policy over the years. Based on over 50 years combined experience of studying and writing on Afrotropical birds, we believe that the *Zoological Record* lists well over 90% of the significant literature on them, both refereed and unrefereed, as well as some of marginal significance. This opinion is supported by Mrs M.J. Thorne (Editorial Manager of BIOSIS, U.K., *in litt.* May 1990) and is not contradicted by Chisman's (1990) findings.

The decrease of interest in and publications on systematics and taxonomy of the Afrotropical biota has recently attracted attention (e.g. Ribbink & Greenwood 1988, Bruton 1989, Crowe et al. 1989, and, on a wider scale, Wilson 1985). Avian systematics has never received much attention in the Afrotropical Region, partly because there are relatively few endemic taxa above the generic level, and partly because much of what has been done has been part of wider studies carried out in the northern hemisphere. In our experience, most of the taxonomic work on Afrotropical birds has been carried out by people unaffected by developments in the last 30 years in the theory and techniques of systematics.

Biogeography, as opposed to purely distributional studies of particular taxa or areas, has never been widely practiced in the Afrotropical Region, perhaps because most workers potentially interested in this field have considered that the work of Chapin (1932) was close to adequate. In the period covered by this review (up to the end of 1980) the principal workers who have dealt with biogeography have been Reg Moreau (e.g. 1966) and Jack Winterbottom (e.g. 1974): neither produced a radical critique of Chapin's work or used new techniques of study.

Natural history or studies of living birds in the wild only approached expectation in the 1940s and exceeded it in the 1960s. This reflects the growing number of ornithologists spending long periods in the Afrotropics or living there permanently, as well as an increasing interest in such matters, as opposed to taxonomic and distributional questions.

The attention paid to six orders (Podicipediformes, Gruiformes, Columbiformes, Strigiformes, Trogoniformes and Coraciiformes) has been substantially in proportion to the number of species they contribute to the Afrotropical avifauna. The tendency has always been for large, conspicuous and economically important groups to receive more attention, either from the 1860s in the case of the Struthioniformes and the Galliformes or from some period in the 20th century.

More curious perhaps is the recent decrease of interest in the Cuculiformes, Caprimulgiformes and Piciformes. With the rise of field studies considerable attention has been given to the Cuculinae breeding parasitically on members of the Passeriformes. Since orders have been included in this analysis when only one is involved in a citation, it is clear that citations on parasitic breeding have reduced the apparent attention given to the Cuculiformes and Passeriformes. This factor does not materially affect the relative lack of attention given to the Passeriformes.

Most of the literature on the Caprimulgiformes has been taxonomic and since this aspect of Afrotropical ornithology is no longer dominant, this order has attracted little attention, not least because field studies on nocturnal birds are difficult to carry out. We are not sure why interest in the Piciformes has decreased.

The relative neglect of the Passeriformes has been a constant in the Afrotropical literature (cf. Craig 1987, 1988). Relative neglect of the Passeriformes is, in fact, a worldwide phenomenon. The similar neglect of the Procellariiformes is due to the fact that all are nonbreeding migrants to the coastal waters and beaches of the Region, mostly in the south. It was only in the 1970s that serious attention began to be given to nonbreeding seabirds in the Region: the African seabird journal *Cormorant* first appeared in 1976.

The rise in the attention given to nine orders (Sphenisciformes, Pelecaniformes, Ciconiiformes, Anseriformes, Falconiformes, Charadriiformes, Psittaciformes, Apodiformes and Coliiformes) is a rectification of earlier lack of attention. In respect of the Psittaciformes there is a large body of literature based on laboratory and captive studies. Another aspect which favours attention to large and conspicuous species is the relative ease in many cases with which statistically significant samples of data may be obtained. This is not usually true for members of the Falconiformes but here interest, often conservation based, has been focused on species at the top of food chains whose numbers and/or ranges have decreased markedly in many cases.

ACKNOWLEDGEMENTS

We, and all ornithologists, are obliged to our predecessors who made time to construct the *Zoological Record Aves* each year in addition to their research work and other duties (Bridson 1968). In chronological order they are: A. Newton 1864-1869,

H.E. Dresser 1870 (part), R.B. Sharpe 1870 (part), 1871-1874, 1882-1883, 1890-1909, O. Salvin 1875-1876, H. Saunders 1877-1881, A.H. Evans 1884-1889, W.L. Sclater 1910-1943, W.P.C. Tenison 1944-1963, A.I. Ivanov 1958-1963 (part). WRS thanks the Foundation for Research Development and the University of Cape Town's Research Committee for financial support. We thank Mrs M.J. Thorne, Editorial Manager of BIOSIS, for photocopies of relevant literature.

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APPENDIX 1

DEFINITIONS OF TOPICS USED TO ANALYZE THEMES IN THE AFROTROPICAL AVIAN LITERATURE

NB These definitions are not always logically mutually exclusive: see Methods.

* indicates topics grouped for the category 'natural history' in Figure 2.

Anatomy - studies of the structure of the soft parts of birds.

*Behaviour - studies on the behaviour of birds, except for restricted studies on breeding, diet, etc.

Biochemistry - studies of the chemistry and chemical functioning of birds' bodies.

Biogeography - studies of the patterns of geographical distribution of birds.

Biometrics - studies of mensural data on parts of birds' bodies or on diet or behaviour.

*Breeding - studies of any aspect of reproduction.

*Communication - studies of information transfer by voice or behaviour.

*Community - studies of coexisting species in particular habitats or restricted areas.

- *Conservation - studies of threats to bird populations, methods of mitigating such threats, and birds of conserved areas.
- Culture - human responses to birds not based on economic necessities.
- Development - studies of morphological or behavioural development of young birds, including in the egg.
- *Diet - studies of what birds eat.
- Distribution - data and studies on where bird species occur.
- Ecology - studies of birds' relations with biotic and abiotic surroundings, usually quantified (seldom used).
- Economics - studies of relations between activities concerned with human livelihoods and birds.
- Environmental Change - studies of the effects of changing environments on birds and their populations.
- Evolution - studies of the effects of natural selection on characters of birds and their speciation.
- Genetics - studies of chromosomal and DNA structures and inheritance of characters.
- *Habitat - studies of faunas or communities associated with particular vegetation assemblages.
- History - history of ornithological activities in the Afrotropical region, from obituaries to ringing reports.
- Identification - aids to identifying bird species in the field.
- Integument - descriptions and studies on the skin and feathers of birds: see also Moults and Oology .
- *Locomotion - studies of flight, diving, walking and other means of movement.
- Migration - studies of migratory movements of birds: often subsumed in Distribution q.v.
- Moult - studies of moult of plumages and feather tracts.
- *Nutrition - studies of the value of different foods eaten by birds.
- Oology - studies of eggs and their external characteristics.
- Osteology - studies of bones and bone systems.
- Paleontology - studies of fossil birds, including archaeological remains.
- *Parasites - studies of external and internal parasites of birds and of birds breeding parasitically on others.
- *Pathology - studies of what kills birds or makes them sick, including countervailing treatments.
- *Pollution - studies of the side effects on birds of economic activities, including pesticides and oil spills.
- Physiology - studies of how living birds' bodies work.
- *Population - studies of bird numbers, sex ratios and breeding productivity.
- *Ringing - studies arising from analyses of ringing recoveries, reports of ringing recoveries.
- Systematics - studies of avian relationships above the generic level.
- Taxonomy - studies of avian taxa at the generic level and below and the names to be applied thereto.
- Techniques - descriptions and studies of methods of achieving research results.

RADIATION IN AFRICAN CANARIES (CARDUELIDAE): A COMPARISON OF DIFFERENT CLASSIFICATORY APPROACHES

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ABSTRACT. Phenetic analyses of skeletal measurements in 44 carduelid species identified three broad phenotypes. Since coefficients of variation are highest in bill measurements, it can be concluded that phenetic relationships are founded primarily on divergence in bill morphology. Each of the three groups extracted has both Afrotropical and non-Afrotropical representatives, indicating that the phenotypes are based on convergent similarity and are thus ecotypes. Phylogenetic analyses based on plumage features and behaviours split the genus *Serinus* (*sensu lato*) into two sister groups, one consisting of Afrotropical seedeaters (genera *Poliospiza* and *Dendrospiza*), the other including Afrotropical seedeaters and canaries (*Ochrospiza* and *Crithagra*), Palaearctic canaries of the genus *Serinus* (*sensu stricto*), rosefinches (*Erythrura*), siskins (*Spinus*, *Carduelis*) and greenfinches (*Chloris*). Plesiomorphic character states in plumage features, as reflected in immature birds, prevail in the Afrotropical Region. **Keywords:** Phenetic relationships, cladistic relationships, skeletal variations, plumage colouration, behaviours, Carduelidae.

INTRODUCTION

The Carduelidae is comprised of about 140 seedeating species, with an almost world-wide distribution. Species richness is greatest in Holarctic (mostly Palaearctic) wooded and bushland biotopes. Siskins (*Spinus*) reach the Neotropics, and a few seedeaters occur in the Oriental Region. Nearly a third of the species occur within the Afrotropical Region, inhabiting dry and moist savannas. Of these, about 35 species are usually lumped within the genus *Serinus* (*sensu lato*) together with several Palaearctic species.

Attempts to sort out African *Serinus* spp. into species-groups have met with some success. On the basis of behavioural characters, five subgroups have been differentiated, calling into question the monophyly of *Serinus* (Nicolai 1960; van den Elzen 1985). The canaries (*Serinus*) are thus mainly distributed in the Palaearctic, one species (*Serinus canicollis*) reaching the southern parts of the Afrotropical Region. Of the remaining species, 27 form (according to courtship display, nestbuilding behaviour and begging calls of the nestlings) four species groups, sometimes separated as four genera: *Ochrospiza* (10 species: *leucopygia*, *menachensis*, *reichenowi*, *xantholaema*, *atrogularis*, *citrinipectus*, *mozambica*, *dorsostrata*, *xanthopygia* and *rothschildi*); *Dendrospiza* (6 species: *citrinelloides*, *hyposticta*, *koliensis*, *scotops*, *capistrata*, *frontalis*); *Crithagra* (4 species: *flaviventris*, *sulphurata*, *donaldsoni*, *albogularis*), *Poliospiza* (7 species: *striolata*, *burtoni*, *leucoptera*, *reichardi*, *mennelli*, *gularis*, *tristriata*), and two genera of uncertain affinity, *Pseudochloroptila* and *Alario*. Genetic distances based on biochemical analyses of proteins and enzymes in seedeating passerines (Stempel 1986) confirmed the closer relationships of Afrotropical species (*Ochrospiza leucopygia*, *O. reichenowi*, *O. mozambica*, *Poliospiza leucoptera*), and

included with them the Eurasian Greenfinch *Chloris chloris* and Bullfinch *Pyrrhula pyrrhula*, rather than two traditionally recognized *Serinus* spp. (*serinus* and *canaria* var. dom.).

In order to elucidate systematic relationships between African species groups, their affinities to the European stock and their adaptive radiation within the Afrotropical Region, two approaches were applied. Phenetic analyses of skeletal measurements were used to study osteological divergence, and phylogenetic analyses of plumage pattern and colouration (including some soft parts) were used to reconstruct phylogenetic histories.

METHODS

Phenetic methods

Phenetic relationships were estimated using a UPGMA (unweighted pair group method using arithmetic averages), Q-mode cluster analysis (Sneath & Sokal 1973). Matrices of correlation coefficients between 44 skeletal measurements of 44 species (49 OTUs, including three species with two subspecies each and two crossbreds) were the basis of all analyses. Matrices were either derived from raw or transformed data (logs and/or partly z-standardized), with all measurements being divided by femur length as a standard. Arithmetic averages of measurements represented species. For more details on morphometrics, see van den Elzen et al. (1987) and Nemeschkal & van den Elzen (1990).

Phylogenetic methods

For the reconstruction of phylogenetic relationships, cladistics is the method of choice. According to cladistic principles only synapomorphies (shared derived character states) contain information about speciation events, and thus are indicators of monophyly (Hennig 1966, Wiley 1981, Ax 1984). Synapomorphies are defined by character polarizations, that is the direction each particular character is thought to have taken during evolution. Two approaches are widely accepted in determining character polarity (Watrous & Wheeler 1981, Crowe 1988): ontogenetic and out-group comparison. Character states possessed by immature phases and/or by sister groups (taxa of more distant relationship than the unit under study) are thought to represent plesiomorphic conditions. Our analyses mainly employed the ontogenetic approach. Nestling plumages in carduelids coincide in some general characteristics, e.g. heavy striation, brownish colours, light bars on the wings, two light spots at cheeks and under the eyes, wing and tail feathers bordered with light margins. They are thought to represent plesiomorphic character states, the condition present in the hypothetical ancestor. Forty-four plumage and one egg colouration characters were employed in this analysis. Thirty-three of the plumage characters were polarized on the basis of nestling phenotype. The remaining characters were unordered. For comparative purposes, only species were included that were also analyzed in the phenetic approach. Character polarizations are summarized in Table 1. Analyses were done with the computer programs PAUP (Swofford 1985) and HENNIG86 (version 1.5: developed by J.S. Farris), that use the parsimony criterion to derive an estimated tree of minimum character transformation steps (Wiley 1981).

RESULTS AND DISCUSSION

Phenetics

The UPGMA analysis clustered species into three broad groupings (Figure 1). Clusters A and B represent smaller and medium sized species (wing lengths 62-80 mm). The first cluster of smaller species (A), comprising a phenotype with blunt bills and shorter legs, is further subdivided into two subclusters, one of Palaearctic species (*Serinus (sensu stricto)*, including the Afrotropical *S. canicollis* and *Alario*, the Linnet *Acanthis cannabina* and the Long-tailed Rosefinch *Uragus sibiricus*), the other smaller Afrotropical species (*Ochrospiza* spp. and *Poliospiza mennelli*). Cluster B unites small to medium sized species characterized by pointed bills and longer hindlimbs. It includes both Palaearctic and Neotropical siskins (*Spinus* spp.), the siskin-like serins (*Dendrospiza*), several *Poliospiza* spp., the Cape Siskin *Pseudochloroptila totta*, the Redpoll *Acanthis flammea* and the European Goldfinch *Carduelis carduelis*. Cluster C unites all species with heavy bills and pronounced mandibles. All larger species are located within this cluster together with smaller, but massively billed species with wing lengths ranging from 66-105 mm. Palaearctic rosefinches (*Erythrura* spp.) and greenfinches (*Chloris* spp.) are combined in several subunits with Afrotropical seedeaters (*Crithagra* and *Poliospiza*) and the Pirol Finch *Linurgus olivaceus*.

Character divergence

Phenetic distance (Camin & Sokal 1965) measures character divergence by the range of the character over the group under study. To verify the amount each character contributes to the phenetic analysis, we compared the coefficients of variation (standard deviation as percentage of the arithmetic mean of all species in each measurement) of all measurements. Generally, the skeletal measurements under consideration can be assigned to three functional complexes: bill and skull elements to the feeding complex, leg and pelvis elements to the hindlimb-locomotion complex, and elements from wing and shoulder girdle to the flying-locomotion complex. Within these functional complexes, coefficients of variation (CV) were highest in the feeding complex and, within this complex, in bill measurements. The CVs of bill measurements (13.40%, average of 7 measurements) were double those of skull measurements (7.80%, average of 11 measurements), pectoral measurements (6.99%, average of 8 measurements) and pelvis measurements (6.83%, 4 measurements). They were almost three times as large as the CVs of leg measurements (4.98%, 3 measurements), and as large as those for measurements of wing bones (13.78%, 6 measurements). Thus, variation in bill dimensions plays a very important role in the carduelid phenotype.

Carduelids are thought to be a phylogenetically young clade, considered by some authors as a family mainly characterized by their feeding habits, especially the ability to cut open and husk dicotyledon seed. Siskin-types employ several foraging techniques and, especially the smaller species, can cling to vegetation. In the species sample chosen, the number of Afrotropical species almost equals the number of non-Afrotropical carduelids. They are also evenly distributed within the three main clusters of the UPGMA analysis. (Cluster A: 11 Afrotropical vs 7 non-Afrotropical species; cluster B: 8 vs 7; C: 9 vs 8). A Komolgorov-Smirnov Two-Sample Test was employed to test whether measurements in the Afrotropical samples had the same statistical distribution as measurements in residual species. Significant congruence exhibited

TABLE 1 - Plumage features, egg colour and ethological characters used in a phylogenetic analysis of carduelid species.

species	character									1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	5	5	5				
	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2				
Dhypo	0	1	1	0	1	1	1	0	1	2	0	1	6	0	0	1	0	0	2	0	0	0	0	0	0	1	1	0
	0	0	0	2	2	1	0	0	1	0	2	1	0	1	0	1	1	1	3	1	2	1	1	0				
Dscot	1	1	1	0	1	1	1	0	1	2	0	1	4	0	1	1	0	0	2	0	0	0	0	0	0	1	1	0
	0	0	0	2	2	2	0	0	1	0	1	1	0	1	0	1	1	1	3	1	2	1	1	0				
Dcapi	1	2	1	0	1	1	1	0	1	2	0	1	2	0	0	1	1	0	2	0	0	0	0	0	0	1	1	0
	0	0	0	2	2	2	0	0	1	0	1	1	0	1	0	9	9	1	3	9	9	9	9	0				
PStot	0	0	0	1	1	1	1	0	2	3	0	1	4	1	1	2	1	0	1	1	1	1	1	1	0	3	1	0
	0	0	1	2	1	1	0	0	0	0	1	2	1	1	0	1	1	1	3	1	0	1	0	1				
Pstri	0	0	0	0	0	0	0	0	0	2	0	1	1	1	1	0	0	0	3	0	0	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	0	0	2	1	1	1	0	0	2	0	3	1	2	4	0	0				
Ptris	0	0	0	1	1	1	1	0	0	2	0	1	1	0	1	0	1	0	3	1	0	1	1	0	0	4	1	0
	0	0	0	2	3	1	0	0	0	0	2	2	1	1	0	0	2	0	3	1	2	4	0	0				
Pleuc	0	0	0	1	1	1	1	0	0	2	0	1	1	1	1	0	1	0	3	0	0	0	1	0	0	1	1	0
	0	0	0	2	2	1	0	0	0	0	2	2	9	9	9	0	2	0	3	9	9	4	9	0				
Pmenn	0	0	0	1	1	1	1	0	0	2	0	1	1	0	1	0	0	0	3	1	0	0	0	0	0	1	1	0
	0	0	0	2	3	1	0	0	0	0	1	1	9	9	9	0	2	0	3	9	9	4	9	0				
Pburt	0	0	0	2	1	1	1	1	0	2	0	1	6	0	0	0	1	0	3	1	0	0	1	0	0	1	1	0
	0	0	0	2	2	1	0	0	1	0	2	2	9	9	9	9	9	9	9	9	9	4	9	0				
SEfla	1	2	1	0	0	0	0	0	1	2	1	2	6	1	0	1	1	0	1	1	0	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	0	0	1	1	1	1	0	0	2	0	3	1	0	4	0	0				
Calbo	0	0	0	0	0	0	0	0	0	2	1	2	1	1	1	0	1	0	2	1	0	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	1	0	2	2	1	1	0	0	2	0	3	1	0	4	0	0				
Csulp	1	2	1	0	0	0	0	0	1	2	1	2	4	1	1	1	1	0	2	1	0	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	1	0	2	2	1	1	0	0	2	0	3	1	0	4	0	0				
Cdona	0	1	1	0	1	1	1	0	1	2	1	2	6	1	0	1	0	0	2	1	0	0	0	0	0	1	1	0
	0	0	0	2	2	1	0	0	0	0	2	1	9	9	9	9	9	9	9	9	9	4	9	0				
Spusi	2	2	2	3	1	1	1	1	1	1	1	2	2	0	1	1	0	0	4	0	1	0	0	0	0	1	1	0
	1	0	0	2	2	1	0	0	0	0	2	2	0	1	1	1	1	1	2	0	0	2	1	0				
Sseri	2	2	1	0	0	0	0	0	1	1	1	2	4	0	0	1	0	0	4	0	1	0	0	0	0	1	1	0
	1	0	0	2	2	3	0	0	0	0	2	2	1	1	1	1	1	1	2	0	0	2	1	0				
Ssyri	2	2	0	0	1	0	1	1	1	1	1	2	4	1	1	1	1	0	4	1	1	1	1	0	0	1	1	0
	1	0	0	2	2	2	0	0	9	9	2	2	9	1	9	9	9	1	2	0	0	2	9	0				
Scani	2	2	0	3	1	0	1	1	1	2	1	2	6	1	0	1	1	0	4	1	1	1	0	0	0	1	1	0
	1	0	0	2	2	1	0	0	0	0	2	2	1	1	9	1	1	1	2	0	0	2	1	0				
Scana	2	2	1	0	0	0	0	0	1	1	1	2	6	0	0	1	1	0	4	0	1	0	0	0	0	1	1	0
	1	0	0	2	2	3	0	0	0	0	2	2	1	1	1	1	1	1	2	0	0	2	1	0				
Aalar	2	2	2	3	1	1	1	1	2	2	0	1	2	1	2	2	1	0	2	1	0	1	1	1	0	4	1	0
	1	1	0	3	3	2	0	0	0	0	1	1	1	1	9	1	1	1	3	0	0	2	0	0				
Oatro	0	0	0	0	0	0	1	0	0	2	1	2	1	0	0	0	0	1	2	1	0	0	0	0	0	1	1	0
	0	0	0	2	1	2	0	0	0	0	2	1	0	1	0	2	2	1	1	1	0	3	1	0				
Oleuc	0	0	0	0	0	1	1	1	0	2	1	4	1	0	1	0	0	1	2	1	0	0	0	0	0	1	1	0
	0	0	1	2	1	1	0	1	0	0	2	2	0	1	0	2	2	1	1	1	0	3	1	0				
Omoza	1	2	1	0	0	1	0	0	1	1	1	2	4	0	0	1	1	1	4	1	0	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	1	0	1	2	0	1	0	2	2	1	1	1	0	1	1	0				
Odors	1	2	1	0	0	0	0	0	1	1	1	2	4	0	0	1	1	1	4	1	1	0	0	0	0	1	1	0
	0	0	0	2	2	3	0	0	1	0	1	1	0	1	0	2	2	1	1	1	0	1	1	0				
Oxant	0	0	0	0	1	1	1	0	0	2	1	2	1	1	0	0	1	1	2	1	0	1	0	0	0	4	1	0
	0	0	0	3	3	1	0	0	0	0	2	2	0	1	0	2	2	1	1	1	0	3	1	0				

CHchl0	0	0	2	1	1	1	1	1	3	1	2	6	1	1	1	1	0	2	1	1	1	1	0	1	2	2	1	
	1	2	0	2	2	1	1	1	1	0	2	2	1	1	9	0	1	0	2	1	0	1	1	0				
CHsin1	2	0	3	1	1	0	1	2	3	1	2	6	1	1	2	1	0	2	1	1	1	1	2	1	3	2	1	
	1	2	0	2	2	1	1	1	9	9	2	2	1	1	9	0	1	0	2	1	0	1	1	0				
CHspi2	2	2	3	0	0	1	0	1	3	1	2	6	1	0	1	1	0	2	1	1	0	1	2	1	2	2	1	
	1	2	0	2	2	3	1	1	1	0	1	2	1	1	9	0	1	0	2	1	0	1	1	0				
Loliv	2	2	2	3	1	1	1	1	1	3	0	1	2	1	0	1	1	0	1	1	0	0	1	0	0	3	1	0
	0	0	0	2	3	2	1	1	9	9	1	2	9	9	9	9	9	9	9	9	9	9	9	9	9	9	0	
SPcuc	2	2	2	3	1	1	1	1	2	2	1	2	2	1	0	2	1	0	4	1	0	0	0	2	1	2	2	1
	1	2	0	2	2	2	0	0	1	1	1	2	1	1	1	1	1	1	2	0	1	3	1	0				
SPbar	2	2	2	3	1	1	1	0	1	1	1	2	3	0	0	1	0	0	4	0	0	0	0	2	1	2	2	1
	1	2	0	2	2	1	0	0	0	0	1	2	1	1	1	1	1	1	2	0	1	3	1	0				
LEarc2	2	0	3	1	1	1	1	2	4	1	3	2	2	1	2	2	0	2	0	0	0	0	0	0	2	4	0	
	1	0	0	3	3	1	1	0	0	1	1	2	1	0	9	9	9	9	9	9	9	9	9	9	9	9	1	
Eeryt	2	2	2	3	1	1	1	1	2	4	1	3	5	0	1	2	0	0	2	0	0	0	0	0	0	3	4	0
	0	0	0	3	3	1	0	1	0	0	1	1	1	0	0	0	1	1	3	0	0	1	9	2				
Emexi	2	2	0	2	1	1	1	0	2	4	1	3	5	0	1	2	0	0	2	0	0	0	0	0	0	4	4	0
	0	0	0	3	3	1	0	0	0	0	1	1	1	0	0	0	1	1	3	0	0	1	0	2				
Usibi	2	2	0	0	1	1	1	1	0	1	1	3	6	0	1	2	0	0	2	0	0	0	0	0	0	4	1	0
	0	0	0	2	1	1	0	0	0	0	1	1	1	0	0	0	1	9	3	0	0	1	9	2				
PRvin0	2	2	2	1	1	1	0	2	4	1	3	6	2	0	2	2	0	1	0	1	1	1	1	0	3	1	0	
	0	0	0	3	3	1	0	0	0	0	1	1	9	9	9	9	9	9	9	9	9	9	9	9	9	9	2	
COcco	2	2	2	3	1	1	1	1	2	3	0	1	2	1	0	2	1	0	1	1	0	1	1	0	0	4	3	0
	0	2	1	3	1	1	1	1	0	1	2	2	0	0	0	0	9	0	2	0	0	1	9	0				
Aflam2	2	0	0	1	1	1	1	0	1	1	3	3	0	0	0	0	0	2	0	0	0	0	0	0	2	1	0	
	1	0	0	2	1	1	0	0	0	0	2	1	0	1	1	1	1	0	3	0	0	1	1	0				
Acann	2	2	0	3	0	0	1	1	2	1	1	3	6	0	1	2	2	0	2	0	0	1	1	0	0	2	3	0
	1	0	0	1	1	1	0	0	0	0	1	2	9	0	9	0	1	9	9	9	9	9	9	9	9	9	0	
CArdu	2	2	2	3	1	1	1	1	2	3	1	4	5	1	2	1	0	2	1	0	1	2	1	3	2	1		
	1	2	1	3	3	2	1	1	0	0	2	2	1	1	9	1	1	0	3	0	1	3	9	0				

Characters and character polarization (9= no comparison): 1. forehead (0-uniform); 2. forehead colouration (0-brown); 3. crown colouration (0-brown); 4. crown pattern (0-striated); 5. ear patch (0-light spot); 6. eye ring (0-present); 7. moustachial stripe (0-present); 8. supercilium (0-present); 9. back colouration (0-brown); 10. back pattern (0-striated); 11. uppertail coverts (0-like back); 12. uppertail coverts colouration (unordered); 13. throat pattern (unordered); 14. flanks (0-striated); 15. breast (0-not contrasting throat and belly); 16. breast colouration (0-brown); 17. breast pattern (0-striated); 18. necklace (0-not present); 19. belly colouration (unordered); 20. undertail coverts (0-striated); 21. undertail coverts colouration (0-not contrasting with belly); 22. wing bar (0-present); 23. wing coverts (0-striated); 24. colouration of primaries (0-uniform brown); 25. pattern of primaries (0-uniform); 26. pattern of secondaries (rear edge) (unordered); 27. colouration of secondaries (unordered); 28. pattern of secondaries (unordered); 29. tail feathers (0-equal); 30. tail pattern (0-uniform brown); 31. rear edge of tail (0-plain); 32. pattern in single tail feathers (unordered); 33. tail colouration (unordered); 34. facial pattern (unordered); 35. bill colouration (0-dark horn); 36. leg colouration (0-dark horn); 37. colouration of juvenile plumage (0-brown); 38. pattern of juvenile plumage (0-heavy striated); 39. sexual dimorphism (unordered); 40. female plumage (unordered); 41. gape colouration of nestlings (0-red-blue-spots); 42. gape rictal colouration of nestlings (0-whitish); 43. bill pattern of nestlings (0-no pattern); 44. nestbuilding (0-solely female); 45. display (unordered); 46. courtship display (0-fluffing-tail up); 47. wing posture during courtship display (unordered); 48. begging calls (0-simple); 49. location call (0-simple); 50. contact call (unordered); 51. nest sanitation (0-nest clean); 52. egg colouration (0-blueish-white).

Abbreviations and species list:

Dhypo - *Dendrospiza hyposticta* and (Dkol) *D. koliensis*; Dscot - *D. scotops*; Dcapi - *D. capistrata*; PStot - *Pseudochloroptila totta*; Pstri - *Poliospiza striolata* and (Pgul) *P. gularis*; Ptris - *P. tristriata*; Pleuc - *P. leucoptera*; Pmenn - *P. mennelli*; Pburt - *P. burtoni*; SEfla - *Serinops flaviventris*; Calbo *Crithagra albogularis*; Csulph - *C. sulphurata*; Cdon (Cdonbuc) *C. (donaldsoni) buehleri*; Spusi - *Serinus pusillus*; Sseri - *S. serinus*; Ssyri - *S. syriacus*; Scani - *S. canicollis* and (Scit) *S. citrinella*; Scana - *S. canaria*; Aalar - *Alario alario*; Oatro *Ochrospiza atrogularis* and (Orei) *O. reichenowi*; Oleuc - *O. leucopygia*; Omoza - *O. mozambica*; Odors - *O. dorsostrata*; Oxant - *O. xanthopygia*; CHchl - *Chloris chloris*; CHsin - *C. sinica*; CHspi - *C. spinoides*; Loliv - *Linurgus olivaceus*; SPcuc - *Spinus cucullatus*;

SPbar - *S. barbatus* and (SPspin) *S. spinus*; LEarc (LEarclit) - *Leucosticte (arctoa) littoralis*; Eeryt - *Erythrina erythrina*; Emexi - *E. mexicana*; Usibi - *Uraquus sibiricus*; PRvin *Procarduelis vinacea*; COcco - *Coccothraustes coccothraustes*; Aflam - *Acanthis flammea*; Acann - *Linaria cannabina*; CArd (CAcar; CAcartschu) - *Carduelis carduelis*, *C. c. tschusii*.

between all measurements ($P < 0.001$) demonstrates that adaptive trends of morphological traits in the two groups converge, despite their inhabiting two biogeographical regions with different biotopes. This confirms that adaptive radiation in carduelids apparently always involves bill diversification. For example, grosbeak-ecotypes are represented in the Afrotropical Region as well as in the Palaearctic (European Grosbeak *Coccothraustes coccothraustes* and African grosbeak seedeaters *Crithagra donaldsoni*, *C. d. buehneri*). This applies also to siskin-like birds (European Goldfinch *Carduelis carduelis*, siskins *Spinus* spp. versus African Citril *Dendrospiza hyposticta* and Cape Siskin *Pseudochloroptila totta*). Thus, phenetic relationships as exhibited in the UPGMA analysis reflect mainly adaptive trends in morphology, primarily bill dimensions, of carduelid species. Species in cluster A exhibit the serin-ecotype, cluster B the siskin-ecotype and C the seedeater-grosbeak-ecotype. That differences in size and bill morphology are the main characters that allow sympatric species to coexist has been verified by principal components analyses (van den Elzen et al. 1987, Nemeschkal & van den Elzen in press).

Phylogenetics

A first analysis of unweighted plumage and egg-colour characters yielded a cladogram with a very low consistency index, suggesting that some of the features coded are adaptations to similar ecological conditions and are plagued by convergence to a similar extent as are skeletal traits. Loss of distinct plumage patterns, marked colours and striation is apparently favoured in open-country biotopes. For example, in several areas of the Afrotropical and Palaearctic Regions, uniformly grey to brownish birds are most commonly found in open habitats, green to yellow coloured species in denser vegetation. Only in this latter group are plumage patterns exhibited in courtship displays, with savanna and semidesert-dwelling species accentuating rather postures and possibly vocalizations.

In order to overcome this high level of homoplasy, plumage characters with high consistency indices were weighted 3-5 greater than those with low CIs. To this data set were added seven behavioral characters (Nicolai 1960, van den Elzen 1985 – Table 1) four of which were polarized using the ontogenetic criterion. This analysis resulted in a cladogram (Figure 2) which is thought to illustrate the best assumption of phylogenetic relationships between the species studied, since species groups of known affinities are united and the cladistic distribution pattern of species (with the exception of *C. coccothraustes*) coincides with biogeographical distributional patterns of the species and genera included (Hall & Moreau 1970). Behaviours and plumage patterns rank *Poliospiza* and *Dendrospiza* species together with *Coccothraustes coccothraustes* and three monotypic African genera, *Alario*, *Pseudochloroptila* and *Linurgus* as a sister group of the remaining Afrotropical, Palaearctic and Neotropical species (Figure 2). Within this second sister group, both greenish *Ochrospiza* species (*mozambica* and *dorsostrigata*) are separated from the remaining greyish-brown members of that genus. They form the sister group to *Crithagra* and the remaining *Ochrospiza* species on the one hand, and all members of the Palaearctic-Neotropical stock (*Serinus*, *Acanthis*, *Leucosticte*, *Erythrina*, *Procarduelis*, *Spinus*, *Carduelis* and *Chloris*) on the other. Neither phylogenetic analysis (using several species as outgroups) split *Serinus* (*sensu lato*) into the distinct species groups indicated by a

comparison of unpolarized behavioural parameters, or placed African species closer to *Chloris* than to *Serinus* as indicated by genetic distances (Stempel 1986). Behavioural characters place *Alario* within *Serinus*. The two other monotypic genera linked to it in the cladogram are of unknown affinity according to their autapomorphic (*Pseudochloroptila*) or unknown (*Linurgus*) ethological attributes (van den Elzen 1985).

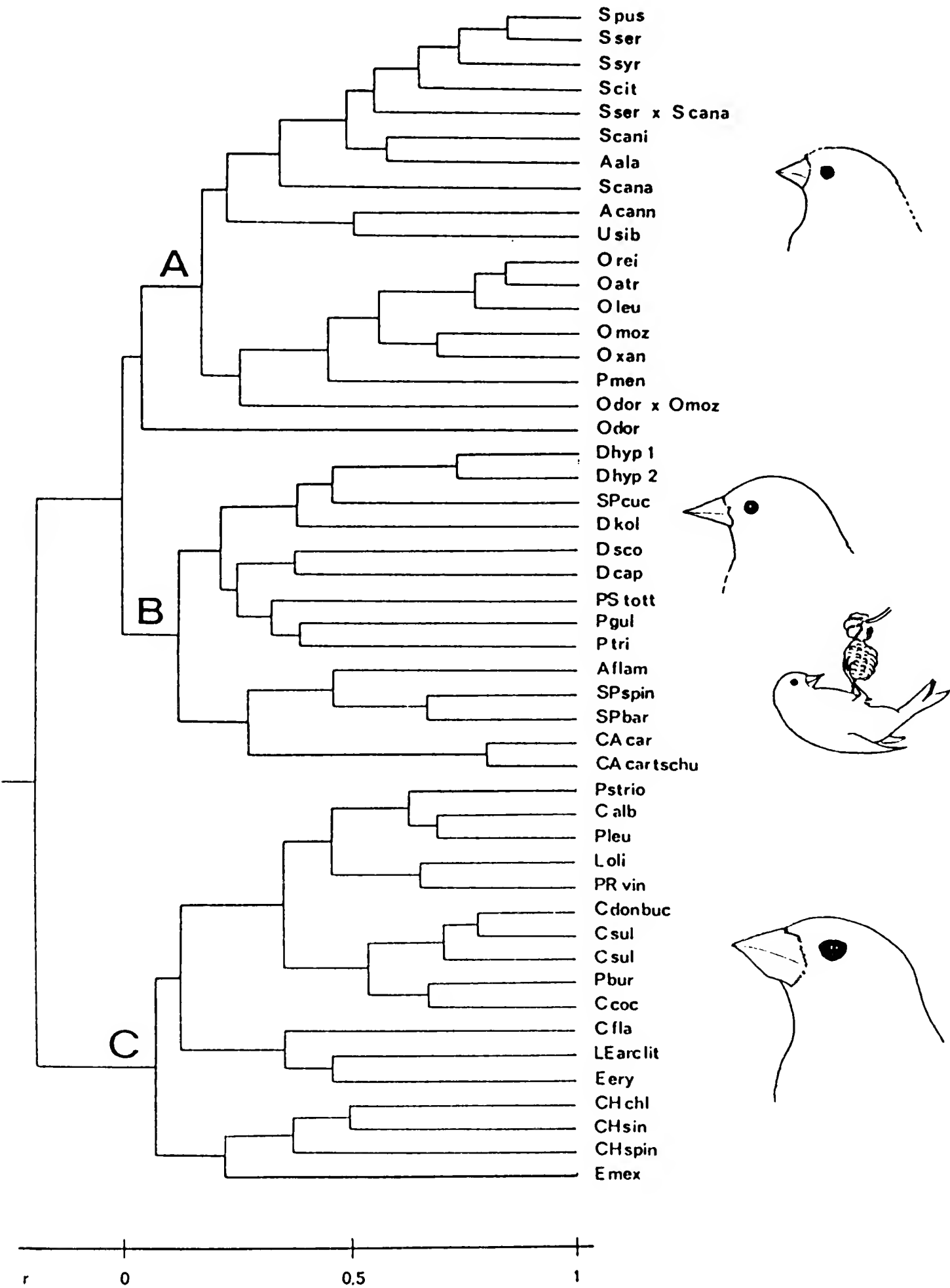


FIGURE 1 - Phenogram of 49 carduelids (44 species, 3 subspecies, 2 crossbreds; UPGMA based on skeletal measurements).

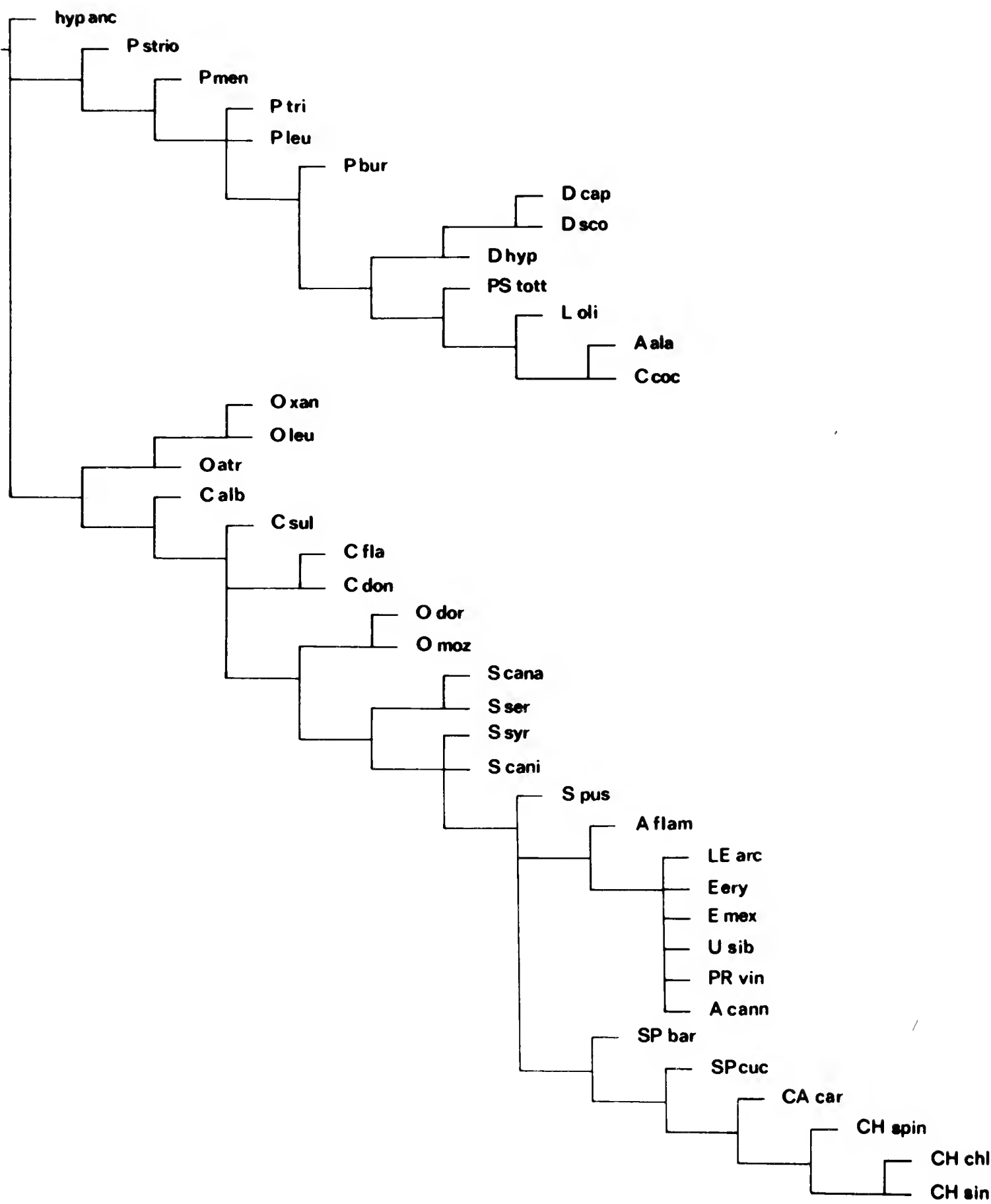


FIGURE 2 - Cladogram of 39 carduelids (five redundant species excluded; HENNIG 86 consensus tree based on plumage characters and behaviours.) .1m1

Biogeographical and taxonomic considerations

In the carduelid species investigated here, plesiomorphic plumage features and behaviours prevail in the Afrotropics, the least anagenetic evolution being found in *Poliospiza*, and partly in *Ochrospiza* and *Crithagra* spp. Apomorphic plumage and behaviours prevail in non-Afrotropical species, being most distinctive in siskins and greenfinches. There are essentially two contradictory approaches employed to correlate evolutionary character states of species with their distributional patterns. According to the classical Darwinian centre of origin concept and the progression rule,

phylogenetically older species, exhibiting plesiomorphic character states are distributed in ancestral centres (Myers & Giller 1988). In the vicariance model, species bearing plesiomorphic features represent ancestral forms, but apomorphic character states of species predominate in developmental centres (Croizat et al. 1974). Ecological concepts link plesiomorphic phenotypes of species with ancestral, unchanged ecological conditions within biotas. The Carduelidae may thus have either dispersed from the Afrotropical Region into the Palaearctic or invaded from the Palaearctic and retained within the Afrotropics, ancestral-like habitats. At least two invasions affected Africa.

This paper does not aim at an update of nomenclature in carduelids. In general, generic names applied coincide with species sets in the cladogram, with the exception of *Ochrospiza*. The grey-coloured species are disassociated from their greenish congeners *O. mozambica* and *O. dorsostriata*, which have been placed between *Crithagra* and *Serinus*. Based on differences in colouration, the two species have been separated as *Microserinus* (Roberts 1922). Cladistic analyses support conclusions drawn from comparative ethology, that the genus *Serinus* (*sensu lato*) as usually applied is paraphyletic, involving at least two species assemblages.

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PICIFORM AFRO-ASIAN ZOOGEOGRAPHY AND SPECIATION

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ABSTRACT. Three piciform families present markedly different tropical Asian-African relations. 26 tropical Asian barbets (three genera, two monotypic) have no near relatives among 42 Afrotropical barbets (seven endemic genera, one monotypic); connections are old and involve *Calorhamphus* and *Megalaima* with *Gymnobucco*, *Stactolaema* and *Pogoniulus*. The Afrotropics have 15 honeyguides of two tribes (four genera, three endemic, one monotypic); tropical Asia has but two species apt to be of recent origin, representing advanced species of *Indicator*. Picids number 52 in tropical Asia (14 genera, nine endemic, three monotypic), versus 26 Afrotropical species (six genera, three endemic, one monotypic); the regions share a forest genus (*Sasia*), wrynecks (*Jynx*), and species of *Picoides* (latter two reach other regions). The two regions have remarkably different picofaunas, with two recent invasions indicated. Both regions have as strong or stronger ties to the Neotropics than to each other. **Keywords:** Piciformes, woodpeckers, barbets, honeyguides, systematics, zoogeography, tropical Asia, Afrotropics, Picidae, Capitonidae, Indicatoridae.

INTRODUCTION

Piciform birds including the woodpeckers (Picidae), barbets (Capitonidae) and honeyguides (Indicatoridae) occur in tropical Africa and Asia. Of these, the Indicatoridae are Palaeontropical, the Capitonidae are pan-tropical and the Picidae are Holarctic, Palaeontropical and Neotropical. The comparison of tropical African and Asian (we use "Asiotropics" to designate the Oriental or Indomalayan Region, as a simplification in accord with use of Afrotropics and Neotropics in the last decade) picofaunas is useful because of occurrence of the three families in both regions, and because these regions do share taxa, even down to the level of species, the lion (*Panthera leo*) being one of the most notable. All families in the group treated herein are universally regarded as closely related, although relations of families are in dispute. All except the nest-parasitic honeyguides nest and roost in usually self-excavated cavities in trees, termitaria or the ground. We consider the barbets to be near the stem of the piciforms that we treat. The honeyguides have specialized features unique to them (e.g. bill hooks in hatchlings), but their behaviour is generally barbet-like, and they have none of the derived features marking the specialized woodpeckers (bill and tail modifications, foraging mode); if they evolved from woodpeckers (e.g. Sibley & Ahlquist 1985), then they did so at a time when ancestral picids had not yet become specialized, i.e. before the origin of the modern subfamilies Jynginae, Picumninae and Picinae of the Picidae.

A general comparison shows these numbers of species in the two regions, with the Afrotropical number given first: Capitonidae (42 vs 26); Indicatoridae (15 vs 2); and Picidae (26 vs 51). Our taxonomy is that of Short & Horne (1985) and Morony et al. (1975) for barbets, Short & Horne (1988b) for honeyguides and Short (1982) for the woodpeckers. We consider no subgroups of barbets to be sufficiently derived to be

separated at the subfamily (Prum 1988) or family (Sibley et al. 1988) levels, except possibly the toucans (Ramphastinae) if they are placed in the same family as the barbets.

RESULTS

Capitonidae

The barbets occur strictly within the limits of the tropics. Their diversity and numbers are greatest in the Afrotropics, unless toucans are considered as barbets, in which case the Neotropics virtually match the Afrotropics. There are seven endemic Afrotropical capitonid genera (*Gymnobucco*, *Stactolaema*, *Pogoniulus*, monotypic *Buccanodon*, *Tricholaema*, *Lybius* and *Trachyphonus*) with species ranging in size from the 10 g tinkerbirds (*Pogoniulus*) to the large-billed, 108 g *Lybius rolleti* and *L. dubius* (Short & Horne 1988a). Noteworthy is their diversity of foraging habits and correlated bill structure (pointed bill, mistletoe-eating *Pogoniulus* spp. to tooth-billed, frugivorous species of *Lybius*, the large species of which have heavy, grooved bills, and the long, narrow, pointed bill of omnivorous *Trachyphonus* spp.). Habitats occupied by Afrotropical barbets are also diverse, with over half the species shunning forests (which are the major habitat of Asiotropical and Neotropical barbets), and some occupying near desert situations (e.g. *Tricholaema melanocephala*), and bushed grassland, where typically feeding on the ground (ground-barbets, *Trachyphonus* spp.).

Asiotropical barbets are far less diverse, with but three genera (*Megalaima*, with 24 species and monotypic *Calorhamphus* and *Psilopogon*). These are forest species largely frugivorous in habits; a few species (e.g. *M. haemacephala*) occur in open second-growth woods, and more species forage in fruiting trees outside of forests in once-forested regions. They range in size from 32 g to 300 g (respectively *M. haemacephala* and *M. virens*). Songs of these barbets are simple hoot, pop or trilling repetitive, often loud notes, as in Afrotropical species of *Gymnobucco*, *Stactolaema*, *Pogoniulus*, *Buccanodon*, and *Tricholaema*; none sings complex, often duetting songs such as those of Afrotropical *Trachyphonus* or *Lybius* spp.

No genera of barbets are shared between these regions, and all genera are endemic to their region; thus, there have been no recent barbet movements between these regions, and connections are apt to have involved ancestral species of Asiotropical *Calorhamphus* and *Megalaima* with those of Afrotropical *Gymnobucco*, *Stactolaema* and *Pogoniulus* at some unknown time in the past. Whether similarities in bill structure and colouration between *Calorhamphus* and *Gymnobucco* are reflective of close relationship or convergence is open to question (Goodwin 1964, Prum 1988). Speciation events within Asiotropical barbets have involved past barriers, as for example the water barriers among Sundaland islands and Southeast Asia (e.g. the *Megalaima armillaris* and *M. chrysopogon* superspecies), insular separations (e.g. Ceylon from India, *M. flavifrons* and its relatives), and Himalayan montane forest separations (e.g. western *M. zeylanica* from eastern *M. lineata* by separation about Nepal). In the Afrotropics, there have been speciation events resulting from past separation of forest blocks by alternating wet and dry cycles (Mayr & O'Hara 1986) within *Gymnobucco* (*peli* and *sladeni*) and *Pogoniulus* (*coryphaeus*, *leucomystax*, *simplex*), but more important by far have been separation of woodland and bushland areas surrounding the forest to the north, east and south, i.e. subregion II and its provinces

and districts of Crowe & Crowe (1982). Most speciation in *Stactolaema* (a woodland offshoot of an ancestor in common with *Gymnobucco*), *Tricholaema*, *Lybius* and *Trachyphonus*, and even some species of *Pogoniulus* (*pusillus* and *chrysoconus*, Short & Horne 1988a) has resulted from separation by forests or by xeric conditions of woodland segments north of the forest in West Africa, to the east of it in the Horn of Africa to East Africa, and to the south of it in southern Africa. Lake Chad in its past enlarged form likely separated *Lybius dubius* west of it and *L. rolleti* to its east. Various species of the *Lybius torquatus* group show signs of evolution through past vicariance events (Short & Horne 1985, Crowe & Kemp 1988) around the forest block from West Africa (*vieillotii*) to the east (*leucocephalus*, *quiffsobalito*) and southward (*rubrifacies*, *chaplini*, *torquatus*). *Tricholaema leucomelas* of southern bushlands interbreeds with *T. frontatus* of the miombo, and, very like *leucomelas*, allopatric *diademata* occurs in East Africa north of the other two.

Indicatoridae

Four genera and 15 species of honeyguides are found in the Afrotropics. The Asiotropics are home to but two species of honeyguides. Friedmann (1955) and Short & Horne (1988b) discussed relationships among species of this largely Afrotropical group. The honeybirds (*Prodotiscus*) are unlike other honeyguides except perhaps little known *Melignomon* in obtaining food as wax from the exudate of scale-insects (Hemiptera: Coccoidea), whereas species of *Indicator* (nine) and virtually congeneric *Melichneutes* feed considerably on beeswax. Asiotropical honeyguides represent only the likely derived (yellow plumage features, rump markings, heavy bill, beeswax dependent) *Indicator* group. The somewhat different bill shape of Himalayan *I. xanthonotus* and Southeast Asian *I. archipelagicus* led Friedmann (1976) to conclude that they represent different invasions of the subgenera *Melanothes* (*xanthonotus*) and *Indicator* (*archipelagicus*) from Africa and Wong (1984) and Payne (1986) followed this up with vocal data, purportedly showing *archipelagicus* related to the *varieaatusindicator* complex of the Afrotropics. Foraging habits, displays and population dynamics of Afrotropical *I. indicator*, *I. varieaatus*, *I. minor*, and *I. meliphilus* (Short & Horne 1990) suggest that *variegatus* is distinctive, and the honeyguiding *I. indicator* is related as closely, or more so, to *I. minor* than it is to *I. variegatus*. Furthermore, *I. indicator* shares only with the two Asian species derived features of colour pattern, namely, enhanced yellow-gold in the plumage, the golden yellow wrist patch (of *indicator* and *archipelagicus*, unique in Piciformes), and the rump patch (of immature *I. indicator*, in which the rump is white to creamy yellow-white, and of *xanthonotus*, in which it is orangish). Parsimony is better served by allowing for one honeyguide invasion of the Asiotropics (while honeyguides could have arisen in the Asiotropics, this would demand wholesale extinctions of all but the most advanced of honeyguides in that region), with differences between *xanthonotus* and *archipelagicus* arising through *in situ* divergence in the shifting Himalayan forests and lowland Southeast Asian forests.

Afrotropical honeyguides remain little known. *Indicator pumilio* and *Melignomon eisenrauti* have been described, *I. narokensis* elevated to species status then synonymized with *I. meliphilus*, *I. conirostris* separated from *I. minor*, and *I. willcocksii* separated from *I. exilis*, all within the past 35 years, and the breeding and hosts of one-third of the species are unknown, as indeed is the case for the Asiotropical species. Thus, speciation patterns within the Afrotropics are unclear, with only broad forest-woodland allopatric speciation, if complete, accepted for *I. conirostris-minor*, and *I. maculatus-variegatus*, although such derivation also is likely for ancestral

Prodotiscus insignis-zambesiae (forest) and *P. regulus* (woodland). Since the major feeding of most Afrotropical honeyguides is on beeswax produced by a single subspecies of the Common Honeybee (*Apis mellifera*), which could have arrived in Africa relatively recently (in geological terms), rapid speciation among *Indicator* and *Melichneutes* is a possibility, if not indeed a likelihood. As for using honeyguide songs as a key to phylogeny, this is not an easy character with which to deal. Songs are variable, and exceedingly alike between some species (e.g. *Indicator conirostris-minor*, *I. maculatus-variegatus*, *I. willcocksi meliphilus*), but quite different in others (e.g. *I. variegatus indicator*, *I. variegatus-minor*, Short & Horne 1988b). Reversions to simple songs, such as a trill, commonly occur in closely related barbets and, when they do take place, they afford no bases for comparisons (e.g. the simple trilled songs-duets of *Trachyphonus vaillantii* are unlike those of all its congeners, and the trilled, buzzy songs of *Lybius minor* and *L. bidentatus* provide no points of comparison with congeners, Short & Horne 1988a). These are vocally equivalent to totally melanic or albinistic plumage shifts with regard to comparisons of plumage pattern among congeners. It seems likely that vocalizations other than songs may be more useful. As examples the chattering guiding call of *I. indicator* is heard from males of *I. variegatus* after copulation, and aggressive calls of *I. minor* rather closely resemble those of *I. variegatus* (pers. obs).

Picidae

Alone among these three piciform families, the Picidae occur in temperate areas, and show a range of adaptations remarkable when one considers their arboreal specialization, for some species are successful on treeless plains (Short 1982). Nearly cosmopolitan, they nonetheless are more speciose and more generally diverse in the tropics than in temperate areas, with the exception of the Afrotropics. They do not cross major water barriers, but they regularly reach near-shore islands, and are diverse on oceanic West Indian islands not reached by barbets. A few picids (*Colaptes* spp., *Sphyrapicus* spp., *Picoides hyperythrus*, *Jynx torquilla*) are highly migratory, as are no barbets or honeyguides.

Asiotropical picids are diverse, representing 14 genera and 52 species, compared with the other major centre of diversity, the Neotropics, with 11 genera in 88 species (Short 1982). There is a sub-centre of picid diversity in the Himalayan area, especially representing *Picus* and *Picoides*, and also *Dryocopus*, that are extensive in distribution throughout the Palaearctic (*Picus*) and even to the Neotropics (*Picoides*, *Dryocopus*), as well as in Asiotropical mountains and lowlands (Short 1983). All three subfamilies are represented in the Asiotropics and the Afrotropics, but the latter has only one piculet (*Sasia africana*, Picumninae) and its 24 species of Picinae represent only four genera, two of which (*Geocolaptes*, *Picoides*) have but one species in that region. Shared species between the Afrotropics and Asiotropics include only the mainly Palaearctic, migratory *Jynx torquilla* and, among genera, only *Sasia* and *Picoides* (Short 1980, 1982; Short & Horne 1988c). The speciose Afrotropical genera *Campethera* and *Dendropicos*, and endemic monotypic *Geocolaptes* have no close Asiotropical relatives except for *Picoides*, likely derived from *Dendropicos* (Short 1980), but rather are tribally related to Neotropical woodpeckers (Short 1985). In particular, Asiotropical Campephilini (*Dryocopus*), Picini (*Picus*, *Dinopium*, *Chrysocolaptes*, *Gecinulus*, *Sapheopipo*, *Blythipicus* and *Reinwardtipicus*), endemic Meiglyptini (*Meiglyptes*, *Hemicircus*, *Mulleripicus*), and *Celeus* of the Colaptini, among the Picinae, and *Picumnus* among the Picumninae have no close relatives in the Afrotropics (Short 1982).

Speciation among Afrotropical woodpeckers has been discussed elsewhere (Short 1980, Short & Horne 1988c). Woodland-grassland versus forest (e.g. *Campethera abingoni* superspecies, *Dendropicos goertae* superspecies, *Dendropicos abyssinicus* superspecies, and megasubspecies within *Dendropicos fuscescens*), east-west forest block separation (*Dendropicos pyrrhogaster* superspecies, *Campethera maculosa* superspecies and megasubspecies of *C. cailliautii*), montane forest isolation (megasubspecies of *C. tullbergi*), and woodland-woodland isolation (*C. punctuligera* superspecies) represent major patterns in recent speciation, and these are in substantial agreement with barriers indicated by guineafowl (Crowe & Crowe 1982), by galliforms generally and by hornbills (Crowe & Kemp 1988), and by other diverse orders of non-passerines (Fry 1988).

DISCUSSION

Afrotropical problems

We will not dwell on these, as all have been mentioned and some discussed (Short 1971, 1980, 1982; Short & Horne 1988c). Serious problems are: 1) the Neotropical relationships of Afrotropical Picidae in contrast to a) sparse relations of the latter with those of the Asiotropics, b) distant relations of Neotropical and Afrotropical barbets, and c) lack of honeyguides in the Neotropics; 2) the presence of a restrictedly forest piculet (*Sasia africana*) having congeneric relatives in the Asiotropical forests, in contrast to sparse picine and distant capitonid relations between the Afrotropics and Asiotropics; and, 3) the apparently recent derivation in the Asiotropics, as far away as Malaysia (where but 13% of lowland forest avian genera are held in common with the wet lowland Afrotropical forest, Wells 1988), from a speciose, advanced genus of Afrotropical honeyguides, with no concomitant barbet, and few possible picid connections, even by dry woodland and scrub taxa.

Here we concentrate on those problems concerning Afrotropical-Asiotropical connections. In the case of the piculet *Sasia africana*, morphology and behaviour certainly indicate that it is congeneric with Asiotropical *S. abnormis* and *S. ochracea* despite its having a (very thin) hallux that is lacking as a derived feature of the Asiotropical species. One assumes that their common ancestor occupied woodland or bushland habitat (unless something of an array of forest sites occurred in an "Arabian pier", Lees-Smith 1986:83), unlike modern species but not unknown in Neotropical species of related *Picumnus* (e.g. *cirratus*, Short 1982). This begs the question, to which we have no answer, of why, if *Sasia* could invade the Afrotropics from Asia, there were not more picid and at least some capitonid invasions of Asia from Africa, given the xeric habitats in the Afrotropics of species of *Dendropicos*, *Campethera*, *Tricholaema*, *Pogoniulus* and *Trachyphonus*? We believe that *Picoides* originated from Afrotropical *Dendropicos*, as we discuss below. The only Afrotropical species of *Picoides* (*P. obsoletus*) occupies wooded grassland and woodland of the Sahel and highland East Africa, but its entry into Africa must have been relatively recent for its morphology is that of the *canicapillus-minor* group of *Picoides* and is unlike that of more *Dendropicos*-like *P. temminckii* and *P. maculatus* (see below).

It seems that: 1) *Jynx*, if it evolved in the Afrotropics, where both species occur, was able to exit to the Palaearctic and fringe of the Asiotropics; 2) an early form of *Dendropicos* entered the Asiotropics from Africa and, after further evolution there,

gave rise to a species able to enter (re-enter) the Afrotropics; 3) Afrotropical-Asiotropical barbet connections occurred long ago, perhaps at the time when *Dendropicos* managed to reach the Afrotropics as nascent *Picoides* spp.; and, 4) likely one species of *Indicator* was able to reach the Asiotropics rather recently, there to become adapted to forest conditions as it spread and differentiated. All of these are subject to review when more data are available on the palaeobotany of the region from the Horn of Africa and the Arabian Peninsula to Pakistan. Lowland piciforms endemic to that critical area number only the picids *Picoides dora* of the Arabian Peninsula and *P. assimilis* of Iran-Pakistan, both of which represent the advanced, redbellied, *major* group of *Picoides* (Short 1982).

Asiotropical problems

The Asiotropical barbets are not related closely to Afrotropical barbets, but all have the repetitive, simple vocalizations typical of Afrotropical *Gymnobucco*, *Stactolaema*, *Tricholaema* and *Pogoniulus* (but not of *Lybius* and *Trachyphonus*). Connections are deemed to be ancient, and perhaps are no closer than they are with Neotropical barbets (Short 1985). The honeyguides present only the problem of one or two invasions from the Afrotropics, and, as we have discussed above, evidence supports the view of one, relatively recent invasion, with subsequent adaptation to forests, *xanthonotus* those of the Himalayas, and rare *archipelagicus*, of rainforests in Greater Sundaland, now restricted to the lowlands. We note that Asiotropical barbets and woodpeckers are larger on average than those of the Afrotropics, and thus many are immune to honeyguide parasitism.

The enigmatic presence in the Asiotropics of a typically patterned (the tail pattern is unique in piciforms) species of otherwise Neotropical *Picumnus* (22 species there), and of a species of otherwise Neotropical (10 species) *Celeus* evades easy explanation and seems to require relatively recent, ex-tropical distribution in the Palaearctic and Nearctic. Palaearctic *Dryocopus martius* and Asiotropic *D. javensis* have Nearctic (one) and especially Neotropical (three) relatives. Restriction of Afrotropical relations to *Sasia africana* (discussed above) and *Picoides obsoletus* is difficult to explain. The latter relates to derivatives of *Dendropicos* in Sulawesi *Picoides temminckii* and Philippine *P. maculatus*, both yellow-shafted in part, a feature found otherwise among piciforms only in many Neotropical Colaptini and Afrotropical Campetherini, including *Dendropicos*. *P. obsoletus* itself seems to represent a less barred and streaked derivative of the common ancestor of these species of *Picoides*, and of *P. canicapillus-moluccensis-minor*.

An intrinsic Asiotropic problem involves, appropriate to this Australasian Congress, the proximity of piciforms to the Asiotropical-Australasian boundary. A number of barbets reach Sumatra, Borneo and Java; only *Megalaima haemacephala* crosses Wallace's line, reaching the Philippines, but it does not occur in Borneo. Four genera of picids have one species reaching the Philippines (widespread *Chrysocolaptes lucidus* and *Dryocopus javensis* and endemic *Picoides maculatus* and *Mulleripicus funebris*); the endemics have as their nearest relatives endemic Sulawesi *Picoides temminckii* (forms a superspecies with *P. maculatus*) and *M. fulvus*. Both Sulawesi endemic piciforms thus are related to Philippine species (the *Picoides* situation went unnoticed by Cracraft 1988). The Philippine-Sulawesi connection is noteworthy zoogeographically, as otherwise *Chrysocolaptes* and *Dryocopus* of the Philippines relate to Borneo, as does Palawan *Dinopium javanense*. No piciform reaches the Sahul edge of Australasia.

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GEOGRAPHICAL MORPHOMETRIC VARIATION IN BIRDS OF THE LOWLAND EQUATORIAL FOREST OF AFRICA

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ABSTRACT. Intraspecific geographical morphometric variation (based on information extracted from the literature) is studied for 216 stenotopic African birds which inhabit lowland equatorial forest. Standard measurements (wing, tail and bill length) were made on samples of selected species from Upper Guinea, Cameroon, western Zaire and eastern Zaire. Geographical variation is present in quite a few species and variation is clinal in some cases, but without any consistent trend. Variation in other species is much more discontinuous. Therefore, geographical variation in the birds studied is unlikely to be an effect of a common ecogeographical rule. Haphazard divergence within forest fragments isolated over geological time seems to be a better causal explanation for this variation. Character displacement is unlikely to have influenced geographical variation in *Bleda* and *Malimbus*, two polyspecific stenotopic forest passerine genera with a different number of species in the several regions.

Keywords: Ecomorphology, geographical variation, Africa, rainforest birds.

INTRODUCTION

Intraspecific geographical morphometric variation occurs in many birds which range widely in latitude (or in altitude) within tropical savanna as well as in temperate regions. For North American species, this variation is sometimes correlated with temperature and humidity, and is often explained (although not in all cases convincingly) by Bergmann's and Allen's ecogeographical rules (Zink & Remsen 1986).

The contemporary climate of lowlands in equatorial tropical Africa, despite a certain amount of regional variation (especially concerning the length of the dry season), is thought to be basically stable (Leroux 1983). Therefore, among the 216 stenotopic lowland forest birds which are resident in this area (Louette 1990), a common ecogeographical explanation for morphometric variation over this narrow latitudinal zone (with negligible seasonal variation in daylength) is very unlikely. But differences in wing (= wing chord), tail and bill (= culmen) length have been documented for 26 nonpasserines (Brown et al. 1982, Urban et al. 1986, Fry et al. 1988) and for at least 20 forest passerines (White 1960, 1961, 1962, 1963) which occupy this area. The presence of such variation, moreover, is also confirmed by the fact that such differences have been used repeatedly as subspecific characters for the species in question.

In the absence of a likely climatic basis for this geographical variation, possibly intraspecific competition could promote ecomorphological variation through character displacement. In species-rich genera with closely related species, the hypothesis that the presence of more sympatric species in a given area should result in more differentiation should be examined. Possible candidates are members of the morphologically homogeneous and stenotopic forest genera *Bleda* (three species in the west - found in one locality (Louette 1981) versus two in the east) and *Malimbus* (seven

species in the centre - locally sympatric (Brosset 1978) versus five in the west and six in the east). This paper investigates the nature and possible causes of intraspecific geographical morphometric variation in stenotopic, lowland forest birds of equatorial Africa.

TABLE 1 - Means in mm (N = 8) for measurements made on African birds of lowland tropical forest. Significant ($P \leq 0.02$ in Mann-Whitney U-test) differences are indicated by '*'. Species that are absent or rare (e.g. *Alethe poliocephala*) are marked as '-'.

Species	Measure- ment	Sex	Regions			
			A	B	C	D
<i>Nectarinia superba</i>	wing	m	69.2*	74.8	75.3	76.3
		f	65.3*	68.6	70.1	70.4
	tail	m	43.7*	46.4	47.3	47.2
		f	41.1	42.6	43.9	42.6
	bill	m	32.4*	36.6	36.6	36.6
		f	32.2*	35.2	36.7	35.6
<i>Andropadus latirostris</i>	wing	m	78.8*	83.8	82.4*	88.1
		f	78.1	77.5	78.3*	83.3
	tail	m	74.1	75.6	75.5*	82.5
		f	73.6	70.6*	74.3*	77.3
	bill	m	17.3	17.9	18.1	17.8
		f	16.4	16.9	17.6	17.0
<i>Alethe poliocephala</i>	wing	m	93.3	91.8	-	89.1
		f	90.1	88.5*	-	85.4
	tail	m	60.8*	58.1*	-	55.6
		f	58.3*	55.3	-	53.8
	bill	m	20.6	20.3*	-	19.6
		f	20.0	19.8	-	19.4
<i>Bleda eximia</i>	wing	m	108.2*	96.3*	105.8	104.9
		f	102.2*	91.3*	97.6	99.4
	tail	m	97.4*	86.0*	95.4	95.4
		f	90.6*	80.8*	89.0	89.4
	bill	m	28.8*	23.3*	24.8	23.2
		f	25.8*	20.9*	23.2	22.7
<i>Bleda syndactyla</i>	wing	m	110.3	111.9*	107.0	106.9
		f	103.5	105.8*	101.3	98.6
	tail	m	93.8*	98.0*	92.8	93.5
		f	88.6*	94.5*	88.7	87.0
	bill	m	29.0	29.0	27.9*	26.1
		f	25.9	25.3	26.4*	24.5
<i>Malimbus nitens</i>	wing	m	89.8	88.4*	93.4*	86.7
		f	82.3	81.8*	87.3*	81.7
	tail	m	57.2*	51.5*	54.5*	49.4
		f	52.9	49.4	51.0*	47.6
	bill	m	23.3*	25.4	24.0	23.3
		f	22.2	23.5	23.8*	22.1
<i>Malimbus malimbicus</i>	wing	m	87.7*	82.8*	89.3*	92.4
		f	82.8*	77.1*	82.4*	85.3
	tail	m	58.5	56.1	55.3	55.7
		f	57.6*	51.6	51.2	50.4
	bill	m	20.4	20.8*	22.3	22.8
		f	19.6	19.9*	21.9	22.3

TABLE 1 – Continued

Species	Measure- ment	Sex	Regions			
			A	B	C	D
<i>Malimbus scutatus</i>	wing	m	88.2*	92.1	-	-
		f	87.9	90.1	-	-
	tail	m	51.9	51.3	-	-
		f	50.4	51.1	-	-
	bill	m	19.2*	20.8	-	-
		f	19.1	19.9	-	-
<i>Malimbus cassini</i>	wing	m	-	89.6	90.5	92.3
		f	-	88.7	88.9	90.1
	tail	m	-	52.3*	49.8	49.4
		f	-	52.7*	49.3	48.8
	bill	m	-	19.8	20.2	20.3
		f	-	19.0	19.9	19.4
<i>Malimbus rubricollis</i>	wing	m	106.5*	103.2	100.2	99.3
		f	101.4	100.4*	94.3	93.9
	tail	m	64.4*	59.5	58.6	58.1
		f	61.6*	58.4*	54.4	54.1
	bill	m	26.0*	23.8	22.8	22.1
		f	24.1	24.3*	22.5	22.0
<i>Malimbus coronatus</i>	wing	m	-	85.9	85.1	87.2
		f	-	84.4	83.8	84.9
	tail	m	-	52.8*	49.3	50.1
		f	-	53.0*	48.5	47.8
	bill	m	-	19.3	19.1	19.1
		f	-	19.5	18.7	19.1

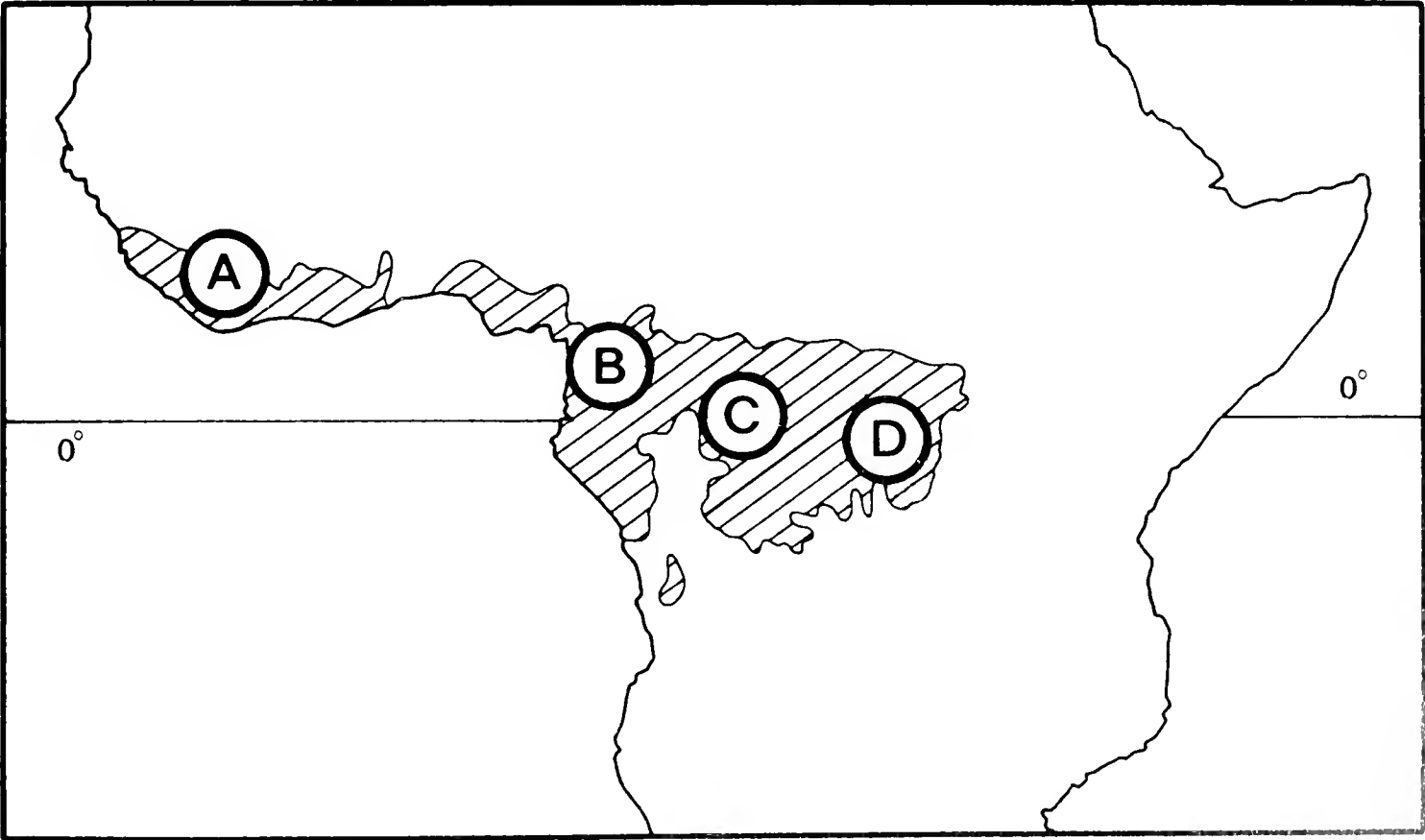


FIGURE 1 - Position of the lowland rainforest in tropical Africa and the locations of the four regions studied.

METHODS

Wing, tail and bill length statistics were extracted from a range of sources cited below, especially "Birds of Africa" and the publications of C.M.N. White. Table 1 lists the species measured by me from four regions in equatorial Africa (see Figure 1) in Tervuren and in the British Natural History Museum: A: Liberia and surroundings; B: lowland Cameroon and eastern Nigeria; C: Equateur Province in Zaire; D: lowlying areas in Kivu Province in Zaire.

These regions cover a rough transect across the African lowland equatorial forest. The three eastern regions are fairly equidistant from one another. However, palaeobiological evidence indicates that region A was (and still is) separated much more effectively from the others than the remaining three have been from one another. These four regions also correspond to the core areas of the important historical forest refugia as defined by Prigogine (1988). The taxa selected here include a species absent in region A and a superspecies with allospecies in contact within region B.

All localities used are below 1000 m a.s.l., with specimens taken over the last several decades, lessening possible altitudinal and temporal bias in mensural variation. Specimens were admittedly prepared by different individuals, but all specimens measured were well-prepared, making differences in measurements resulting from variation in preparation methods unlikely. Sample size consisted of eight male and eight female specimens (adult skin specimens only) from each region.

Wing length was measured using a stopped ruler, tail length and bill length were measured with calipers; all to the nearest 0.5 mm.

Thorpe (1976) and Zink & Remsen (1986) have reviewed approaches to the study of geographical variation. In this study, because of the relatively small sample sizes involved, interregional and intersexual comparisons were made with a non-parametric test (Mann-Whitney U-test, critical value at $P \leq 0.02$).

RESULTS

From results published in the literature (Table 2), it appears that geographical morphometric variation is not limited to particular taxonomic groups nor to a single measurement. However, intraspecific variation in wing length is most often noted, probably because it is one of the most frequently published measurements, differing by up to 10%. Moreover, there is no consistent 'trend' in the variation detected (Table 2), although parallel trends (not necessarily both statistically significant) were found for most species in both sexes, with males nearly always being markedly larger.

A geographical cline?

The results in Table 2 suggest that there may be some general trend which could be interpreted as clinal, with longer billed, winged and tailed birds in the eastern regions; but is this trend real? For example, for *Nectarinia superba* (a sexually dichromatic species) the sample from region A is smaller in all three measurements than those from the three eastern samples, between which there are no significant differences.

TABLE 2 - Lowland Afrotropical forest bird species in which there is marked intraspecific geographical variation in at least one body measurement.

West < East
<i>Accipiter castanilius</i> : wing A-C<D
<i>Accipiter erythropus</i> : wing A<B-D
<i>Francolinus lathamii</i> : wing A-C<D
<i>Poicephalus gularis</i> : wing, bill A<B-D
<i>Psittacus erithacus</i> : wing A<B-D
<i>Glaucidium tephronotum</i> : wing A-B<C-D
<i>Halcyon badia</i> : wing A<B<C<D
<i>Bycanistes fistulator</i> : wing A<B-D
<i>Tropicranus albocristatus</i> : wing A<B-D
<i>Tockus fasciatus</i> : wing A<C-D
<i>Tockus camurus</i> : wing A<B-D
<i>Pogoniulus scolopaceus</i> : wing A<C-D
<i>Gymnobucco bonapartei</i> : wing B<C<D
<i>Bleda syndactyla</i> : bill A-C<D (Chapin 1953)
<i>Andropadus latirostris</i> : wing A<B<C<D (Chapin 1953)
<i>Nectarinia superba</i> : wing A<B<C<D (White 1963)
West > East
<i>Tauraco macrorhynchus</i> : wing A>B
<i>Centropus leucogaster</i> superspecies: wing, bill A>B-C>D
<i>Raphidura sabini</i> : wing A>B-D
<i>Dendropicos gabonensis</i> : wing A>B-D
<i>Alethe poliocephala</i> : wing A-C>D (White 1962)
<i>Malimbus nitens</i> : wing, bill A<B-C>D (Chapin 1954)
Complex
<i>Phoeniculus bollei</i> : wing A-C<D, bill A-C>D
<i>Ploceus aurantius</i> : wing A>B<C-D (Chapin 1954)

This suggests that the variation is not clinal (contra White 1963). In fact, ecomorphologically, the sample from region A must be considered as quite distinct from the others, despite this species' geographically uniform colouration. This is an example of morphological and temporal covariance, because region A was separated historically from the conglomerate of the three other regions. Wing and tail length in another species, *Andropadus latirostris*, also do not vary clinally, increasing from west to east. In fact, the sample from region D is the only one statistically larger than the others (contra Chapin 1953). *Alethe poliocephala* shows a general decline from west to east for all three measurements, although mean values for regions A and B are not significantly different for wing and bill length. Unfortunately for statistical purposes, too few specimens are available from region C, where this species is very rare. However, this fact may also give a clue to the cause of this possible clinal variation, in suggesting that this bird is philopatric.

Although each of the three above mentioned species belongs to a genus, polyspecific in the forest, interspecific competition as a cause of size variation can be ruled out, because the number of species in these genera is equal in all four regions (Louette 1990).

Genera with different numbers of sympatric species

BLEDA. *B. eximia*: the sample in region A has larger means for all three measurements than that from region B which, in turn, is smaller than the one from region C. Samples from regions C and D are not significantly different. Bill length for the sample from region A is larger than that for samples from the three other regions. *B. syndactyla*: samples from all four regions are rather similar in dimensions, the one from region B having the longest wing and tail lengths, and the one from region D having the shortest bill length. In region A, where three species co-occur (including *B. canicapilla*: wing, males: 102.7; females: 93.7; tail, males: 93.6; females: 84.9; bill, males: 24.0; females: 22.3 mm), *B. eximia* has a particularly long bill and *B. canicapilla* has a relatively very short bill. This may possibly be a result of character displacement or simply a result of the long separation of the population of *eximia* in region A from the eastern ones. *B. syndactyla* does not have the largest measurements in region A, has the longest tail length in region B, and is not significantly different from the other two species in wing and bill length within A and B. *B. eximia* has the smallest measurements in region B. In summary: in region B, the two remaining species seem to have diverged from one another, but this is not the case in regions C and D.

MALIMBUS. There are insufficient specimens available for *M. racheliae* (no measurements taken, it is the smallest species in the genus, see Serle 1954) which is endemic to region B. Also, in the superspecies *M. ballmanni/ibadanensis/erythogaster*, there are too few specimens from the three western regions; (for region D: wing, males: 92.4; females: 88.3; tail, males: 55.1; females: 54.2; bill, males: 24.4; females: 22.8 mm; its dimensions are quite close to those of *M. malimbicus*).

Some *Malimbus* spp. exhibit apparently haphazard patterns of geographical variation. In *M. nitens* for example, the specimens from region D have short tails, whereas those from region C have long wings. For *M. malimbicus* samples, wing length is relatively small in region B and increases both towards the east and towards the west, especially in the west, resulting in a markedly different wing/tail length ratio. On the other hand, bill length is longer in the two eastern populations of this species.

Geographical variation in the superspecies *M. scutatus/cassini* is particularly complex: in the west, wing and bill lengths for *scutatus* increase (weakly) towards the contact area with *cassini*, whose dimensions are a close match with those of its allospecies. In *cassini*, tail length decreases in the eastern portions of its range. In *M. rubricollis*, all three measurements tend to decrease from west to east, although mean values for regions C and D are not significantly different. This is the longest-winged and stoutest-billed species in the genus, so, it is surprisingly even larger in region A, in which there are fewer sympatric congeners than in region B. In regions B, C and D, a smaller species, *M. coronatus* is uniform in these three measurements, possibly indicating relatively recent contact and gene flow over geological time.

Region B, the most 'crowded' region, does not appear to harbour more marked interspecific divergence, except maybe for bill length in *M. nitens*. According to Brosset (1978), in region B, *coronatus* and *cassini* are canopy-dwellers, but they are of the same size in regions B, C and D, and so is the other species, *scutatus*, their ecological counterpart in region A.

DISCUSSION

Intraspecific geographical morphometric variation in birds of the African equatorial forest appears to be a common phenomenon. It is unlikely (and most difficult to test) in the species with small ranges, but the bulk (156 of the 216) of the species studied have ranges which encompass most of the forest block (Louette 1990). Among this subset of the avifauna, the number of species with variable size may be larger than listed in Table 2. Many species are known by few specimens so that size variation may be undetected and (possibly in small passerines) measurement error may mask actual variation. Moreover, the unexpected nonconcordant variation between sexes found in some species may be due to incorrect sexing of specimens in species without sexual dimorphism. In *Malimbus*, with sexual dimorphism in plumage, trends in both sexes are similar, with relatively smaller differences between sexes.

None of the regions studied here have a preponderance of large or small populations of the species studied. In fact, each of the four regions harbours the largest population of at least one species, disproving the possible action of a general ecogeographical rule. Although variation in the most marked examples in the literature (Table 2) might suggest the existence of an west-to-east clinal increase in size, the detailed studies conducted here do not support such a general trend. Indeed, one wonders if these morphometric regional differences may have, in part, a non-genetic basis in this biome, as was demonstrated for temperate regions (James 1983). Nevertheless, the existence of such variation in the relatively stable African equatorial forest emphasizes the need for research of this nature on a global scale.

There are only a few publications which have dealt specifically with morphometric variation in tropical African birds. In his classic paper on *Pyrenestes* (not a stenotopic forest genus), Chapin (1924) found regional morphometric differences (in bill measurements especially) which were correlated with rainfall and vegetation. The shortest bills were found in birds from the highest rainfall areas. However, if this correlation between environment and morphology has some causal basis, one would expect several species to exhibit the same pattern. I conclude provisionally, because abiotic factors are fairly stable year round in the forest biome, that the observed variation is more likely either to have a non-genetic basis or is a result of haphazard changes that occurred in forest fragments isolated during geological time.

The concept of character displacement, i.e. morphological variation enhanced through competition with congeners does not find much support among the species studied here. There is only one possible instance (mentioned above) in the genus *Bleda*. In the much more speciose genus *Malimbus*, although there are of course ecological differences between the species (Brosset 1978), there is no evidence of character displacement.

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MORPHOMETRICS OF THE FALCONIFORMES: AN OVERVIEW

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ABSTRACT. Morphometrics of the 291 species and 79 genera of Falconiformes was studied by taking 24 measurements on a virtually complete series of ten specimens of 280 species and 14 distinctive subspecies. A cluster analysis based on these measurements for all taxa, separating males and females of dimorphic species, is presented. Species judged subjectively or shown in other studies to be similar morphometrically are also clustered together in this study. Twenty-eight percent of species were distinctive, including 68% of the 41 monotypic genera in the order. Examples of phylogenetic or ecomorphological convergence are suggested by comparison with systematic arrangements and biogeographic distributions of the species. Taxa in most clusters are allopatric, suggesting little overlap in size and niche within, but considerable convergence between, areas.

Keywords: Falconiformes, morphometrics, convergence, ecomorphology, systematics.

INTRODUCTION

The size and proportions of an organism indicate the ecological niche which it occupies, but similarities of design between organisms may reflect either common ancestry or convergence. Overall similarity of design has been included previously in deciding the phylogeny of the 291 species of Falconiformes¹ (Kemp & Crowe 1990), which may be why their relationships have been poorly resolved. This paper analyses the morphometrics of 280 species in the order to establish objectively which species are most similar to one another in size and proportions. The analysis, together with systematic arrangements and biogeographic distributions of the species, supports the existence of convergent designs between related species, unrelated species, and species occupying different biogeographical areas.

METHODS

Twenty-four measurements of the head (8), wing (4), legs (2), feet (8) and tail (2) (Biggs et al. 1978) were taken on 280 falconiform species. Species not included were the Eastern Honey Buzzard *Pernis ptilorhynchus*, Kinabalu Serpent Eagle *Spilornis kinabaluensis*, Swamp Harrier *Circus approximans*, Blue and Grey Sparrowhawk *Accipiter luteoschistaceus*, Grey-headed Goshawk *A. princeps*, Dwarf Sparrowhawk *A. nanus*, Ovambo Sparrowhawk *A. ovampensis*, New Britain Collared Sparrowhawk *A. brachyurus*, Pacific Black Hawk *Buteogallus subtilis*, Javan Hawk Eagle *Spizaetus bartelsi* and Black Caracara *Daptrius ater*. We attempted to measure 10 specimens of each species, five of each sex and all of the same subspecies. Full samples were obtained for 225 species plus 14 distinctive subspecies. Only for 12 species were

¹ Classification, scientific names and distribution follow Amadon & Bull (1988), as amended by Kemp & Crowe (1990).

fewer than five specimens measured (Madagascar Serpent Eagle *Eutriorchis astur* (3), Black Harrier *Circus maurus* (4), Nicobar Sparrowhawk *Accipiter butleri* (4), Imitator Sparrowhawk *A. imitator* (1), Semicollared Sparrowhawk *A. collaris* (3), Cuban Hawk *A. gundlachi* (2), Papuan Goshawk *A. meyerianus* (4), Ridgway's Hawk *Buteo ridgwayi* (3), Rufous-tailed Hawk *B. ventralis* (2), Lined Forest Falcon *Micrastur gilvicollis* (2), Buckley's Forest Falcon *M. buckleyi* (4) and Western Red-footed Falcon *Falco vespertinus* (4)).

The mean for each measurement was calculated for each species. For the 171 species in which there was a bimodal size distribution, the larger specimens were assumed to be females (f) and the smaller males (m), and the sexes were analyzed separately. The 478 sets of means for all species, subspecies and sexes were compared by BMDP2M logged phenetic cluster analysis (Dixon 1985). Details of the samples taken are available from A.C.K. and of the analyses from T.M.C.

RESULTS

An overview of the cluster analysis for all species, subspecies and distinctive sexes is presented as a dendrogram (Figure 1 after Literature Cited), with six major (A-F) and 41 minor (A1-8, B1-7, C1-7, D1-10, E1-8, F1) clusters. The species within each cluster are listed within genera, and the order in and between genera does not indicate the exact branching sequence nor, therefore, their exact degree of similarity.

DISCUSSION

Inspection of the genera, species and subspecies within each cluster (Figure 1, Appendix) shows that the measurements do reflect overall similarity of design within similar size classes (e.g. by clustering together: large or small members of *Accipiter* (A1, A4, B2, B6, D2, E8) and *Falco* (A7, B1, B3, B4, B5, D8); *Milvus*, *Haliastur*, *Pernis*, *Henicopernis* and *Lophoictinia* (D6); *Machaerhamphus* with large *Falco* species (D9); *Geranospiza* with *Circus* (A5); *Micrastur* with different sizes of *Accipiter* and *Buteo*-like species (A2, A4, B2, D7); *Parabuteo* with large *Accipiter* species (D2, E8)). No specific attempt was made to reduce effects of size in the analysis since, together with proportions, they are important in defining the ecomorphological niche for each raptor design and, hence, separating the sexes of many dimorphic species. The effects of size would have to be reduced to examine similarities of design between species of different size. The analysis also supports morphometric similarities that have been shown in other, more detailed studies (e.g. of *Asturina* by Millsap 1986, of *Accipiter* by Wattel 1973, of *Falco* by Cade 1982, Boyce & White 1987). However, our results extend these studies by including all species of Falconiformes and so making possible objective inter-generic comparisons.

Our analysis indicates distinctive designs by:

- 1) placing genera separately from other groups of species (monotypic *Pandion* (E1), *Machaerhamphus* (D9), *Neophron* (D1), *Sagittarius* (C7), *Terathopius* (C7), *Sarcorhamphus* (C6), *Gypaetus* (C5), *Gampsonyx* (B7), *Chelictinia* (A8), *Elanoides* (A8), *Morphnus* (E2), *Ictinaetus* (E2), *Eutriorchis* (D7), *Herpetotheres* (D4), *Geranospiza* (A5), *Kaupifalco* (A2), *Busarellus* (E5), *Hamirostra* (E4),

Erythrotriorchis female (E2), *Harpyopsis* male (C2); ditypic *Polyboroides* (E1), *Rostrhamus* (D10), *Daptrius* (D10); all species of *Elanus* (A6), *Microhierax* (plus African Pygmy Falcon *Polihierax semitorquatus* (F1)), *Cathartes* (plus *Coragyps* (D1)),

- 2) linking species of similar design (independent of phylogenetic affinity) (*Necrosyrtes* and *Gypohierax* (D1); *Gymnogyps* and *Vultur* (C5); *Pithecophaga* and female *Harpia* (C4); males of Taita Falcon *Falco fasciinucha*, Oriental Hobby *F. severus* and Bat Falcon *F. ruficularis* (B1); female Taita Falcon *F. fasciinucha* and males of Orange-breasted Falcon *F. deiroleucus*, Grey Falcon *F. hypoleucos*, Barbary Falcon *F. pelegrinoides* and Peregrine Falcon *F. *Peregrinus peregrinus** and *F. P. minor* (A7)) or,
- 3) placing morphologically distinct species separately from other groups (Rufous Crab Hawk *Buteogallus aequinoctialis* (D7), Black-breasted Snake Eagle *Circaetus gallicus* (E1), Slaty-backed Forest Falcon *Micrastur mirandollei* (A2), Collared Forest Falcon *M. semitorquatus* (D7), Lesser Fishing Eagle *Ichthyophaga humilis* (E4), Brahminy Kite *Haliastur indus* (D6), Rough-legged Hawk *Buteo lagopus* male (E3), Martial Eagle *Hieraaetus bellicosus* female (C1) and Long-tailed Hawk *Urotriorchis macrourus* female (D10)).

A few genera have all or most of their species within one larger cluster (*Butastur* (A2), *Gyps* (C6), *Aviceda* (A3), *Harpagus* (B3), *Incitina* (B4)) and a few species are widely separated from other members of their genus (New Zealand Hobby *F. novaeseelandiae* male with *Accipiter* (A4), Aplomado Falcon *F. femoralis* female with *Aviceda* (A3)). These distinctive forms include 28% (81) of the 291 species, all members of 48% (38) of the 79 genera but 68% (28) of the 41 monotypic genera in the Falconiformes. The many mono- and ditypic genera that are shown to be morphometrically distinctive support the contention that most previous raptor classifications have placed more emphasis on form than on relatedness (Kemp & Crowe 1990).

Examination of the biogeographic realms represented within each minor cluster (Figure 1), together with knowledge of the detailed distribution of each species (Amadon & Bull 1988), indicates that species of similar design, by size or proportions, are allopatric. It also indicates where convergence, and presumably ecological replacement, occurs between different biogeographical realms (e.g. males of Taita Falcon, Oriental Hobby and Bat Falcon from Afrotropical, Indomalayan and Neotropical realms respectively (B1); large and small *Haliaeetus* species and Greater Fishing Eagle *Ichthyophaga ichthyaetus* from all but the Neotropical realm (C1, C2); buzzard-like *Leucopternis*, *Asturina*, *Rupornis*, *Kaupifalco*, *Butastur*, *Melierax* and *Spilornis* among *Buteo* species of Neotropical, Afrotropical and Indomalayan realms (A2, D3); large *Buteo* species of the Holarctic (E3)). The allopatry and geographical replacement between species of similar design also suggests that our measurements are related to morphological features of importance in the ecology of the Falconiformes.

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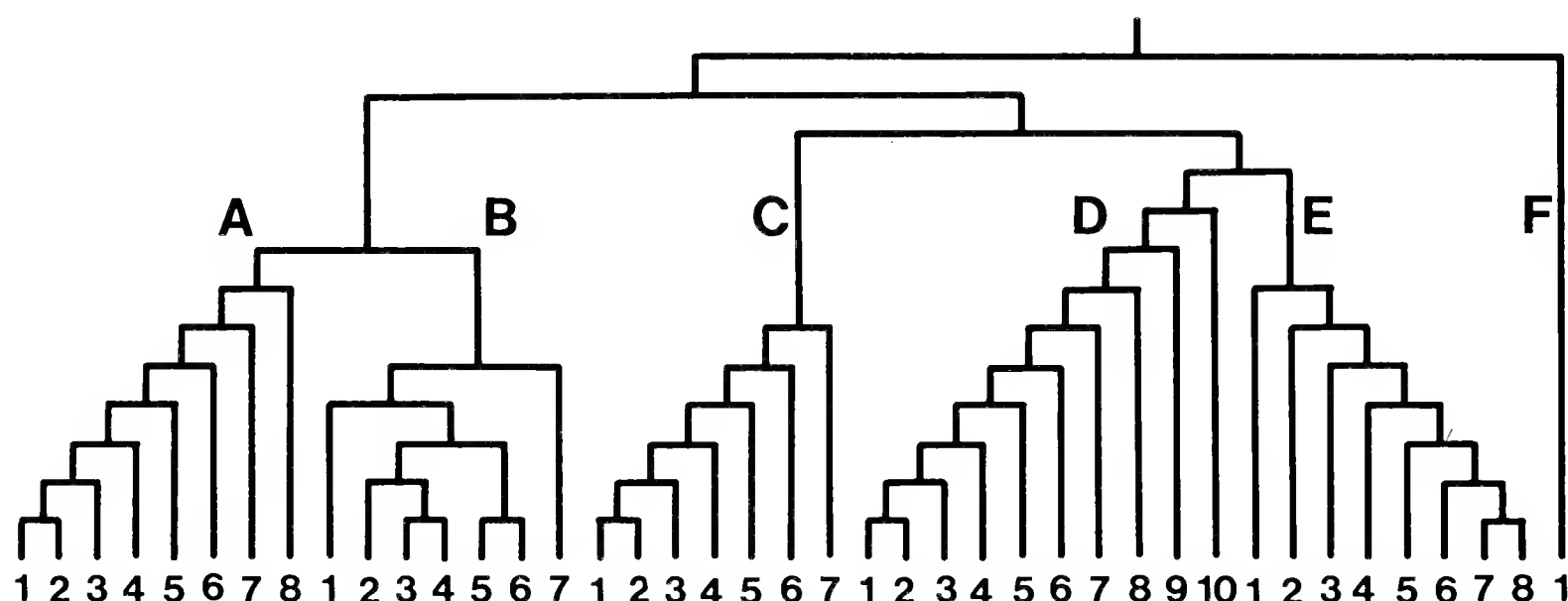


FIGURE 1 - A cluster analysis of 280 falconiform species based on 24 measurements and the biogeographic realms occupied by species (nominate subspecies unless indicated, m - only male, f - only female, PA Palearctic, AF - Afrotropical, IM - Indomalayan, WA Wallacean, AU - Australasian, NA - Nearctic, NE Neotropical, non-breeding migrant range in brackets).

A1.

Accipiter (*albogularis* f,AU; *melanochlamys* f,AU; *gundlachi* m,NA; *bicolor* f,NE; *trivirgatus* IM,WA; *tachiro* f,AF; *fasciatus* AU; *melanoleucus* m,AF; *novaehollandiae* m,AU; *nov. griseogularis* f,AU; *poliogaster* f,NE; *cooperi* f,NA)

A2.

Kaupifalco monoarammicus AF
Micrastur mirandollei NE

Buteo (*bra. albigula* m,NE; *ridgwayi* NE; *platypterus* NA(NE); *leucorrhous* NE)
Butastur (*teesa* IM; *indicus* PA(IM,WA); *liventer* IM,WA; *rufipennis* AF)
Rupornis magnirostris NE
Leucopternis (*semitlumbica* NE; *plumbea* NE; *melanops* NE; *kuhli* NE)
Asturina nitida m,NA,NE

A3.

Aviceda (*jerdoni* IM,WA; *madagascariensis* MA; *subcristata* AU; *cuculoides* AF)
Falco femoralis f,NA,NE
Milvago (*chimachima* NE; *chimanao* NE)
Chondrohierax uncinatus NE

A4.

Accipiter (*bicolor* m,NE; *nisus* f,PA(AF,IM); *tachiro* m,AF; *madagascariensis* f,MA; *rufiventris* f,AF; *cooperi* m,NA(NE); *cirrhocephalus* f,AU; *erythrauchen* AU; *rhodogaster* f,WA; *henicogrammus* m,AU; *poliogaster* m,NE; *henicogrammus* f,AU; *doliocephalus* f,AU; *francesii* m,MA; *nov. griseogularis* m,AU; *nov. hiogaster* f,AU; *tach. macroscelides* f,AF; *melanochlamys* m,AU; *haplochrous* f,AU; *rufitorques* f,AU; *albogularis* m,AU)
Micrastur buckleyi NE
Falco n. novaeseelandiae m,AU

A5.

Geranospiza caerulescens NE
Circus (*pygargus* PA(AF); *maurus* m,AF; *cinereus* m,NE *melanoleucos* m,PA(IM,WA); *cyaneus* m,PA,NA; *macrourus* m,PA(AF,IM);)

A6.

Elanus (*leucurus* NA,NE; *scriptus* AU; *notatus* AU; *caeruleus* PA,AF,IM,WA)

A7.

Falco (*fasciinucha* f,AF; *hypoleucos* m,AU; *pelegrinoides* m,PA; *peregrinus* m,PA; *per. minor* m,AF; *deiroleucus* m,NE)

A8.

Elanoides forficatus NA,NE
Chelictinia riocourii AF

B1.

Falco (*fasciinucha* m,AF; *severus* m,IM,WA,AU; *rufigularis* m,NE)

B2

Accipiter (*bad. dussumieri* IM; *castanilius* f,AF; *poliocephalus* m,AU; *rufitorques* m,AU; *haplochrous* m,AU; *brevipes* PA(AF); *butleri* f,IM; *nov. hiogaster* m,AU; *francesii* f,MA; *f. brutus/griveaudi* f,MA; *collaris* m,NE; *tach. macroscelides* m,AF; *gularis* f,PA(IM,WA); *griseiceps* m,WA; *imitator* f,AU; *superciliosus* f,NE)
Mionisus gabar AF
Micrastur (*ruficollis* NE; *gilv. plumbeus* NE)

B3.

Harpagus (*bidentatus* NE; *diodon* NE)
Falco (*cenchroides* AU; *moluccensis* IM,WA; *rup. fieldi* AF; *tinn. rupicolus* AF,PA,IM; *rup. arthuri* AF; *zoniventris* MA; *dickinsoni* AF; *rufigularis* f,NE; *severus* f,IM,WA,AU; *concolor* PA(MA); *subbuteo* PA(AF); *longipennis* m,AU; *cuvierii* AF; *columbarius* PA,NA; *chiguera* AF,IM; *punctatus* MA)
Spizapteryx circumcinctus NE

B4.

Falco (*alopex* AF; *rupicoloides* AF; *longipennis* f,AU; *femoralis* m,NA,NE; *ardosiaceus* AF; *eleonora* PA(MA))
Ictinia (*mississippiensis* NA,NE; *plumbea* NE)
Aviceda leuphotes IM

B5.

Falco (*amurensis* PA(AF,IM); *vespertinus* PA(AF); *araea* MA; *naumanni* PA(AF); *sparverius* NA,NE; *newtoni* MA)
Polhierax insignis IM

B6.

Accipiter (*erythropus* AF; *minullus* AF; *superciliosus* m,NE; *cirrhocephalus* m,AU; *rufiventris* m,AF; *striatus* NA,NE; *nisus* m,PA(AF,IM); *rhodogaster* m,WA; *virgatus* m,IM,WA; *madagascariensis* m,MA; *gularis* m,PA(IM,WA); *badius* AF; *f. brutus/griveaudi* m,MA; *soloensis* PA(IM,WA))

B7.

Gampsonyx swainsonii NE

C1.

Aegyptius (*calvus* IM; *occipitalis* AF)
Haliaeetus (*albicilla* PA; *leucocephalus* NA; *pelagicus* m,PA; *leucoryphus* f,PA,IM)
Aquila (*heliaca* f,PA,IM; *audax* AU; *gurneyi* AU; *verreauxii* AF; *chrysaetos* PA,NA)
Harpyopsis novaeguineae f,AU
Harpyhaliaetus coronatus NE
Spizaetus (*isidori* f,NE; *coronatus* f,AF)
Hieraaetus bellicosus f,AF
Harpia harpyja m,NE

C2.

Harpyopsis novaeguineae m,AU
Haliaeetus (*leucogaster* IM,WA,AU; *sanfordi* AU; *vocifer* AF; *vociferoides* MA)
Ichthyophaga ichthyaetus IM,WA
Spizaetus (*isidori* m,NE; *nipalensis* f,IM; *coronatus* m,AF)
Hieraaetus fasciatus PA,IM

C3.

Aquila (*heliaca* m,PA,IM; *rapax* AF; *clanga* PA,IM(AF))
Geranoaetus melanoleucus NE
Harpyhaliaetus solitarius NE
Haliaeetus leucophrys m,PA,IM
Circaetus cinereus AF

C4.

Harpia harpyja f,NE
Pitheophaga jeffreyi WA

C5.

Gypaetus barbatus PA,AF
Gymnogyps californianus NA
Vultur gryphus NE

C6.

Gyps (*bengalensis* IM; *africanus* AF; *indicus* IM; *fulvus* PA; *himalayensis* IM,PA; *rueppellii* AF; *coprotheres* AF)
Haliaeetus pelagicus f,PA
Aegyptius (*tracheliotus* AF,PA; *monachus* PA)
Sarcorhamphus papa NE

C7.

Terathopius ecaudatus AF
Sagittarius serpentarius AF

D1.

Cathartes (*aura* NA,NE; *melambrotus* NE; *burrovianus* NE)
Coragyps atratus NA,NE
Neophron percnopterus PA,AF,IM
Necrosyrtes monachus AF
Gypohierax angolensis AF

D2.

Accipiter (*gentilis* m,PA,NA; *henstii* m,MA; *buergersii* m,AU; *meyerianus* m,AU; *n. novaehollandiae* f,AU; *gundlachi* f,NA;)
Erythrotriorchis radiatus m,AU
Parabuteo unicinctus m,NA,NE
Megatriorchis doriae m,AU

D3.

Phalcoboenas (*megalopterus* NE; *carunculatus* NE)
Hieraaetus (*morphnoides* m,AU; *pennatus* m,PA,IM,AF)
Buteo (*solitarius* NE; *albonatatus* f,NA,NE; *auguralis* AF; *swainsoni* NA(NE); *polyosoma* m,NE;
brachypterus MA; *oreophilus* AF; *lineatus* NA,NE; *but. vulpinus* PA,AF; *bra. albigula* f,NE;
brachyurus NA,NE)
Circus (*buffoni* m,NE; *spilonotus* PA(IM),AU; *aeruginosus* m,PA; *maillardi* m,MA; *ranivorus* f,AF)
Spizaetus nanus IM
Melierax (*poliopterus* AF; *canorus* AF; *metabates* AF)
Spilornis (*minimus* IM; *elgini* IM; *ch. holospilus* WA; *ch. rufipectus* WA)
Dryotriorchis spectabilis AF
Leucopternis (*schistacea* NE; *lacernulata* NE)
Asturina nitida f,NA,NE

D4.

Herpetotheres cachinnans NE

D5.

Circus (*cinereus* f,NE; *macrourus* f,PA,AF,IM; *cyaneus* f,PA,NA; *ranivorus* m,AF; *melanoleucus*
f,PA(IM,WA); *maurus* f,AF; *assimilis* m,WA,AU)

D6.

Haliastur (*indus* IM,WA,AU; *sphenurus* AU)
Pernis (*apivorus* PA(AF),IM; *celebensis* WA)
Milvus (*migrans* PA,AF,AU; *mig. parasitus* AF; *milvus* PA; *mig. lineatus* IM)
Lophoictinia isura AU
Henicopernis (*longicauda* AU; *infuscata* AU)
Leptodon cayanensis NE

D7.

Urotriorchis macrourus m,AF
Micrastur semitorquatus NE
Eutriorchis aster MA
Buteogallus aequinoctialis NE

D8.

Falco (*biarm. fledeggii* PA; *mexicanus* NA; *per. peali* NA; *rusticolus* PA,NA; *cherrug* PA; *subniger*
AU; *deioleucus* f,NE; *per. peregrinus* f,PA; *Pelegrinoides* f,PA; *Per. minor* f,AF;
novaezeelandiae f,AU; *hypoleucus* f,AU; *jugger* IM; *biarmicus* AF; *berigora* AU)

D9 .

Machaerhamphus alcinus AF

D10.

Daptius americanus NE
Rostrhamus (*hamatus* NE; *sociabilis* NA,NE)
Urotriorchis macrourus f,AF

E1.

Polyboroides (*typus* AF; *radiatus* MA)
Circaetus (*gallicus* PA,IM; *gal. beaudouini* AF; *gal. pectoralis* AF)
Pandion haliaetus PA,NA,IM,WA,AU,(NE,AF)

E2.

Erythrotriorchis radiatus f,AU
Spizaetus (*tyrannus* NE; *philippensis* f,WA; *ornatus* f,NE; *lanceolatus* f,WA; *nipalensis* m,IM;
cirrhatu f,IM,WA)
Hieraaetus (*spilogaster* AF; *kienerii* f,IM,WA)
Spizastur melanoleucus f,NE
Morphnus guianensis NE
Ictinaetus malayensis IM,WA,AU

E3.

Buteo (*hemilasius* PA(IM); *regalis* NA; *rufinus* PA,IM; *lagopus* PA,NA)

E4.

Aquila (*pomarina* PA(AF); *pom. hastata* IM)

Spizaetus occipitalis AF

Buteo (*galapagoensis* f,NE; *ventralis* m,NE; *rufofuscus* f,AF; *aug. archeri* f,AF)

Spilornis cheela IM

Buteogallus urubitinga NE

Polyborus plancus NE

Phalcoboenas australis NE

Ichthyophaga humilis IM

Hamirostra melanosternon AU

E5.

Busarellus nigricollis NE

E6.

Circus (*aeruginosus* f,PA; *assimilis* f,AU,WA; *buffoni* f,NE)

E7.

Hieraaetus (*wahlbergi* AF; *morphnoides* f,AU; *pennatus* f,PA,AF)

Buteo (*galapagoensis* m,NE; *albonotatus* m,NA,NE; *poecilochrous* NE; *jamaicensis* NA; *polysoma* f,NE; *ventralis* f,NE; *aug. archeri* m,AF; *rufofuscus* m,AF; *albicaudatus* NA,NE)

Buteogallus (*meridionalis* NE; *anthracinus* NA,NE)

Leucopternis (*occidentalis* NE; *albicollis* NE; *princeps* NE; *polionota* NE)

Circaetus (*fasciolatus* AF; *cinerascens* AF)

E8.

Spizaetus (*africanus* AF; *lanceolatus* m,WA; *ornatus* m,NE; *philippensis* m,WA; *cirrhatu* m,IM,WA; *alboniger* IM)

Hieraaetus (*ayresii* AF; *kienerii* m,IM,WA)

Spizastur melanoleucus m,NE

Megatriorchis doriae f,AU

Accipiter (*henstii* f,MA; *melanoleucus* f,AF; *meyerianus* f,AU; *gentilis* f,PA,NA; *buergersii* f,AU)

Parabuteo unicinctus f,NA,NE

Circus maillardi f,MA

Microhierax (*melanoleucos* IM; *fringillarius* IM; *erythrogonss* WA; *caerulescens* IM; *latifrons* IM)

Polihierax semitorquatus AF

SYMPOSIUM 5

**PATTERNS AND PROCESSES OF POPULATION
DIFFERENTIATION IN BIRDS**

Conveners A. J. BAKER, G. F. BARROWCLOUGH
and D. T. PARKIN

SYMPOSIUM 5

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INTRODUCTORY REMARKS: PATTERNS AND PROCESSES OF POPULATION DIFFERENTIATION IN BIRDS

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INTRODUCTION

Patterns and processes of population differentiation have been the subject of intensive investigation by researchers around the world in the latter half of this century. The focus for this work has been the neo-Darwinian assertion that processes of population differentiation can be extrapolated through time to account for the origin of new species. Understanding of these processes is fundamental to systematics and evolutionary biology because only then can we begin to generalize about intraspecific variation, population histories, and speciation.

In the last 20 years, considerable progress has been made in documenting patterns of population differentiation in birds, utilizing sophisticated statistical techniques. Inferences from these patterns suggest that adaptive differentiation occurs rapidly via short bouts of strong directional selection. New developments in statistical methods will lead to critical reappraisal of patterns and processes of differentiation at the morphological level.

Inferences about processes of morphological differentiation of populations have been largely untestable, however, because of the complexity of experimentation with the quantitative genetic system that controls development. The central question in assessing the adaptive significance of geographic variation in characters is what portion is under genetic control and thus is amenable to the action of natural selection? Innovative experimental transplants of eggs between different populations of Red-winged Blackbirds have demonstrated that a significant amount of the size differentiation between populations is nongenetic. This discovery emphasizes that future studies need to partition variation into genetic and environmental components, and to investigate their patterns of covariation among populations.

New perspectives on patterns and processes of population differentiation are now emerging from direct studies of nuclear and mitochondrial genetic systems. Protein electrophoresis of a wide range of avian species has established that effective population sizes of birds are mostly in the order of 10^2 - 10^3 , and that differentiation is promoted by random drift, especially when geographic barriers prevent homogenizing gene flow between populations.

The analysis of sequence variation in mitochondrial DNA (mtDNA) is an exciting new tool for elucidating population genetic structure, dispersal, and historical biogeogra-

phy. New clues about population histories of birds, heretofore unobtainable from nuclear genes or morphology, are arising because mtDNA evolves much faster than nuclear DNA and is inherited as a haploid female clone. Matriarchal phylogenies unobscured by recombination can thus be used to trace population histories, and bottlenecks can be detected because mtDNA is much more sensitive to reductions in effective population size than are nuclear genes.

Morphometric, developmental, and genetic approaches have already produced new insights into patterns and processes of population differentiation in birds. This symposium will summarize knowledge in these fields, and provide examples of active areas of current research.

THE DESCRIPTION OF GEOGRAPHIC VARIATION IN BIRD POPULATIONS

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ABSTRACT. Studies of geographic variation in birds that have involved museum skins and skeletons have emphasized pattern of variation; those involving molecular techniques have emphasized quantity of variation. Methods are proposed, such as PCA on allelic frequencies and nested ANOVA on morphometric traits, that will facilitate comparisons over different sets of characters and across taxa. Some methodological problems are listed that require further investigation.

Keywords: Genetic differentiation, geographic variation, morphometrics, principal components, variance partitioning, *Atlapetes personatus*, *Strix occidentalis*.

INTRODUCTION

The study of geographic variation in avian populations has become increasingly more statistical over time. Early in this century, the results of such studies were restricted to descriptions of new subspecies or re-evaluations of existing ones (e.g., Oberholser 1915). At that same time, however, statistics itself was just developing as a discipline. By the middle decades of the century, studies of geographic variation included reports of coefficients of variation — a measure of intrapopulation variation — as well as frequency distributions of characters across populations (e.g., Miller 1941). The inclusion of simple tests of significance followed and, in more recent years, the use of simultaneous multiple comparisons and multivariate descriptive techniques have become nearly universal (e.g., Johnson 1980). These latter procedures involve laborious calculations and transformations of the original observations, and consequently necessitate the use of computers and statistical packages. The methodology is commonly referred to as morphometrics.

A second development also occurring in the last couple of decades has been the use of “biochemical” or “molecular” techniques, such as electrophoresis, for revealing presumed genetic variation within and among populations (e.g., Barrowclough 1980). These methods also have led to analyses that are intricate and computer dependent. A few particularly intensive studies of geographic variation in birds have involved both multivariate morphometrics and molecular approaches (e.g., Zink 1986).

It is curious that practitioners of these two research programs have largely emphasized different aspects of geographic variation. The morphometricians have tended to produce descriptions of patterns of variation over geographical and morphological space. The former might be considered an extension of “traditional” surveys of geographic variation; the apotheosis of such studies might be James’ (1970) presentation of trend surfaces for eastern North American birds in which, for example, contours of wing-length are superimposed on a map. Power’s (1970) study of geographic variation in the Red-winged Blackbird *Agelaius phoeniceus* is another fine example that

involves more elaborate statistical testing. For an example of the latter, see Baker (1985: Figure 3).

On the other hand, studies using molecular genetics have been largely concerned with the estimation of quantity of variation. This follows, perhaps, as a natural consequence of the tendency of these studies to be used for phylogenetic inference. For example, estimates of the magnitude of the among-locality component of genetic variance (F_{st}) are frequently reported (Barrowclough 1983) along with estimates of various genetic distances. When patterns of molecular variation over geography are sought, they are most commonly presented as an hierarchy, for example using clustering techniques (e.g., Baker & Moeed 1987).

There are elements here of a classic dialectic; however, the morphometric-pattern versus molecular-quantity viewpoints need not be in opposition. For example, any specific instance of geographic variation can be thought of as a set of patterns each associated with a magnitude, like vectors. Parts of this resolution have always been present; eigenvectors, for example, are associated with magnitude, an eigenvalue, and the routine clustering of taxa on the basis of genetic distance implies the existence of pattern, if only hierarchical. Nevertheless, I believe this perspective has been missing in studies of avian infraspecific variation. Perhaps a couple of examples will better illustrate the problem.

VARIATION IN THE SPOTTED OWL

The Spotted Owl *Strix occidentalis* has a more or less linear range along the Pacific coast of North America from southern British Columbia to southern California with a second, disjunct portion of the range from the states of Utah and Colorado south to Michoacán in Mexico. In studying geographic variation in this species (Barrowclough 1991b), I took seven standard museum specimen measurements, e.g., culmen length, wing and tail lengths, etc. A second set of six characters involved aspects of plumage pattern including the barring and spotting of feathers. For example, one such measurement was the width of the pale band on the outer tail feather. A third set of data was the color ranking I assigned each individual based on comparison with a series of specimens varying from light to dark brown. Finally, a fourth data set consisted of the frequency of alleles at an Esterase-D locus based on electrophoresis. These various data were available from individual specimens from British Columbia to central Mexico. The individuals were grouped into populations based on geographic contiguity and sample size; population means were then computed for the various characters.

For data such as these, one might typically look for patterns of geographic variation by plotting population means vs. locality. The results of such an exercise are shown in Figure 1a for two presumably unrelated mensural characters for males: culmen length and middle toe claw length. It is evident that these two characters convey concordant information about pattern of variation — both character plots form two sets of localities separated by a disjunction in size. This concordance suggests that, for some reason, bill and toe length are not free to vary independently; that is, perhaps there is a latent, possibly genetic, factor in these owls — overall size — that simultaneously affects all mensural characters. Principal component analysis (PCA) is a way —

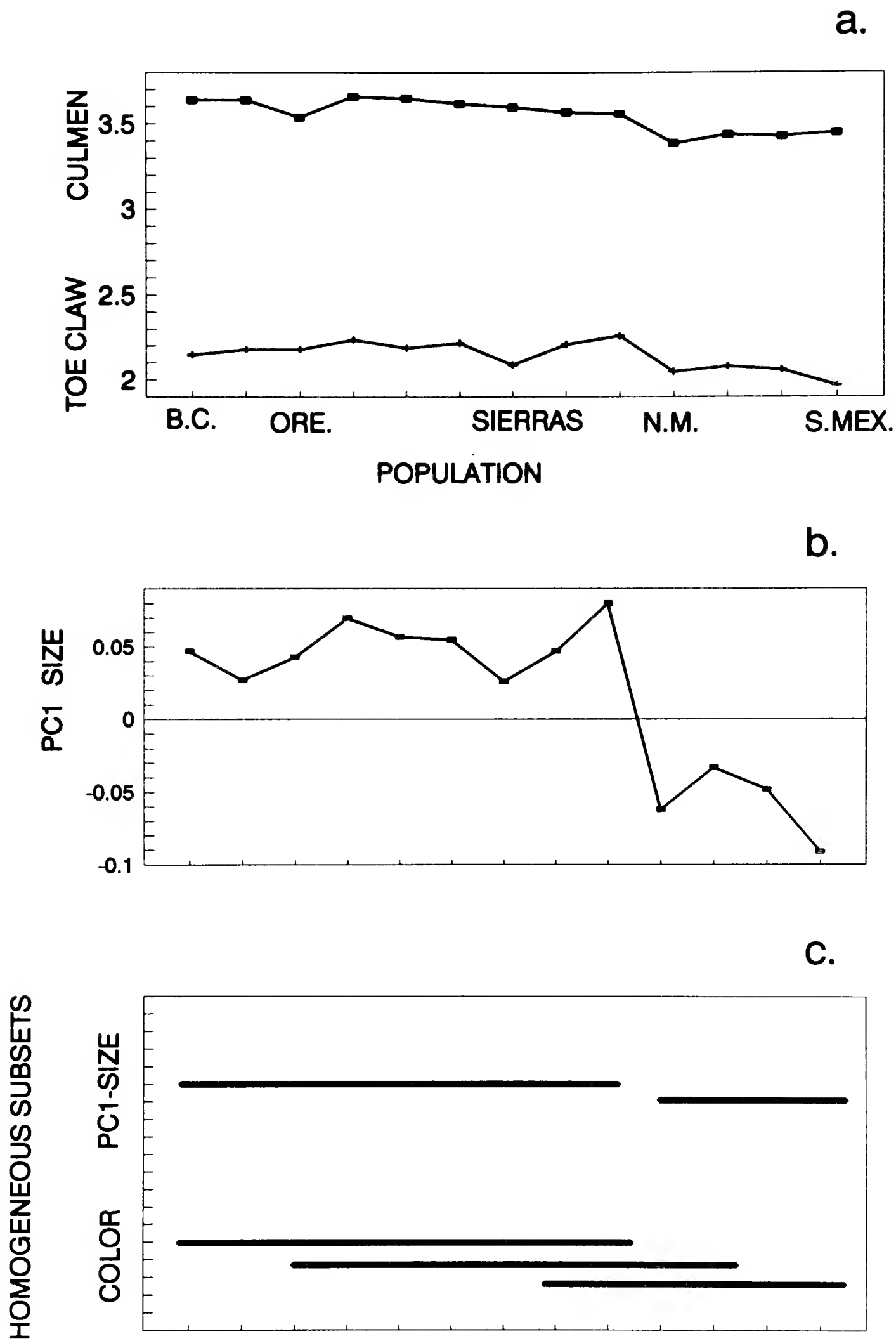


FIGURE 1 – Patterns of geographic variation in male Spotted Owls. a: plot of mean culmen and middle toe claw lengths (cm) versus locality from British Columbia to central Mexico. b: plot of mean score on principal component 1 for standard skin measurements vs. locality. c: homogeneous subsets of localities as indicated by SS-STP analysis for PC1 and color scores. (BC = British Columbia; ORE = Oregon; NM = New Mexico; SMEX = Southern Mexico.)

widely available, but not necessarily the best — to search for such dependencies and the underlying latent variables (Bookstein et al. 1985). In the case of the standard measurements on these owls, a PCA on the covariance matrix of log-transformed character means of the populations indicated that the first multivariate component accounted for 50% of the total variation. This new variable is also plotted in Figure 1b. The plot confirms the existence of an overall factor, which we might refer to as “size” because of the large positive contributions of the linear measurements to the axis. This factor divides the localities into two size classes concordant with the major gap in the species’ range.

A statistical test to confirm the pattern we have inferred is possible. One can obtain the scores of individual specimens from all of the populations on the among-locality PCA axis. The population means and standard deviations of these scores allow one to perform a sums of squares-simultaneous test procedure (SS-STP); this is a multiple comparison test that maintains an overall specified significance level (Gabriel & Sokal 1969). In this case (Figure 1c), the test confirmed the existence, at the .05 level, of two homogeneous, non-overlapping subsets of localities.

Similar analyses can be performed on the plumage pattern and plumage color data sets. In the case of plumage color, the analysis was univariate; for the plumage pattern measurements, the variation in the several characters was again found to lack independence and a PCA revealed the existence of a single axis accounting for 67% of the total variation. However, for these two data sets, the pattern of geographic variation among populations was clinal rather than being organized into the two discrete subsets found for the “size” variables. SS-STP analyses of both the univariate color and first PCA axis for the plumage pattern reflected this trend in identifying several overlapping homogeneous subsets rather than the two disjoint ones discussed above (e.g., Figure 1c).

The last of the four data sets for the Spotted Owl consisted of allelic frequencies (Barrowclough & Gutiérrez 1990). The usual way to analyze these data is to compute the fraction of the total variation distributed among populations; F_{st} , a statistic developed by Wright (e.g., 1978) provides such an estimate. At the Esterase-D locus, one allele was fixed in the Pacific coast populations of the owls; an alternate allele occurred at a frequency of 0.611 in New Mexico populations. The consequent estimate of F_{st} was 0.55; this indicates that 55% of the total variation is distributed among populations, and 45% within.

VARIATION: PATTERN AND MAGNITUDE

These results, as briefly outlined in the above example, are roughly typical of studies of this sort. Note that I have described patterns of variation for the three data sets involving traditional study specimens, and magnitude of variation for the molecular data. This makes it difficult to compare the results of the two types of characters; further, the fact that the three descriptions of pattern have no magnitude associated with them makes comparison difficult both inter se as well as with other taxa.

The description of patterns of geographic variation of molecular data is not particularly novel, but is not frequent in avian studies. Allelic frequencies, e.g., \hat{p}_i , are quan-

titative data with non-traditional distributions – binomial, for example. A transformation such as $\hat{Y}_i = \sin^{-1} \sqrt{\hat{p}_i}$ (Sokal & Rohlf 1981) removes the dependency of the variance of the frequency on the mean. PCA can then be performed, for example, on all but one of the allelic frequencies per locus to find overall patterns of genetic variation over geography. Barrowclough and Johnson (1988) have briefly discussed and illustrated this approach for a couple of cases in birds. The logic behind the approach is straightforward: each genetic locus is presumably an independent character. Therefore, one would not expect a principal component to explain a large amount of the total variation unless some factor had acted in common across loci. Selection, mutation, and drift should not do this; but gene flow or its opposite, isolation, will. Thus, PCA on allelic frequencies is a method for inferring historical patterns of migration and isolation. For the Spotted Owl example, the situation is trivial; the single varying locus results in an essentially binary pattern among geographic regions — attributable to isolation — that is similar to that obtained for “size” and will not be illustrated here.

The estimation of the magnitude of patterns of mensural variation has received even less attention. Consider two questions involving comparisons: first, Johnston and Selander (1964) described rapid (less than 100 years) differentiation in the phenotype of populations of introduced House Sparrows *Passer domesticus* in North America. How does the extent of this differentiation compare to that found in native North American taxa such as the relatively undifferentiated Chipping Sparrow *Spizella passerina* and the well-differentiated Song Sparrow *Melospiza melodia*?

Second, in the example of the Spotted Owl, both the Esterase-D locus and a general size factor indicated disjunction corresponding to allopatric portions of the range. In the case of the molecular data, 55% of the total variation was distributed among the regions; what was the equivalent portion for size?

One way to think about both of these problems is in terms of variance partitioning. After all, the F_{st} for genetic data is just the result of an ANOVA standardized for a particular kind of non-Gaussian variation. An hierarchical (nested) analysis of variance on the mensural characters or color ranks, for example, could provide the requisite comparative results. This is the approach originally adopted by Johnston (1976) following the lead of his colleague Sokal; however, the idea has not received much further attention. It was briefly alluded to in reviews by Baker (1985) and Zink and Remsen (1986). In the case of the owls, such an analysis indicated that 58% of the variance in the general size variable was distributed between the two regions, 1% among localities within regions, and 41% within localities (error term). For the color ranks, the corresponding results were: between regions - 35%, among localities - 11%, within localities plus error - 55%. Finally, for the first pattern PC axis: between regions - 58%, among localities - 13%, within localities plus error - 29%. These results suggest that, for all four disparate sets of characters, a third to a half of all variation was distributed between the two regions. Johnston's (1976) report on variation in skeletal characters of House Sparrows is the only study of which I am aware that has produced a similar analysis in avian systematics, albeit on univariate characters and without an hierarchy; nevertheless, the technique seems useful for furthering the development of a comparative science of geographic variation.

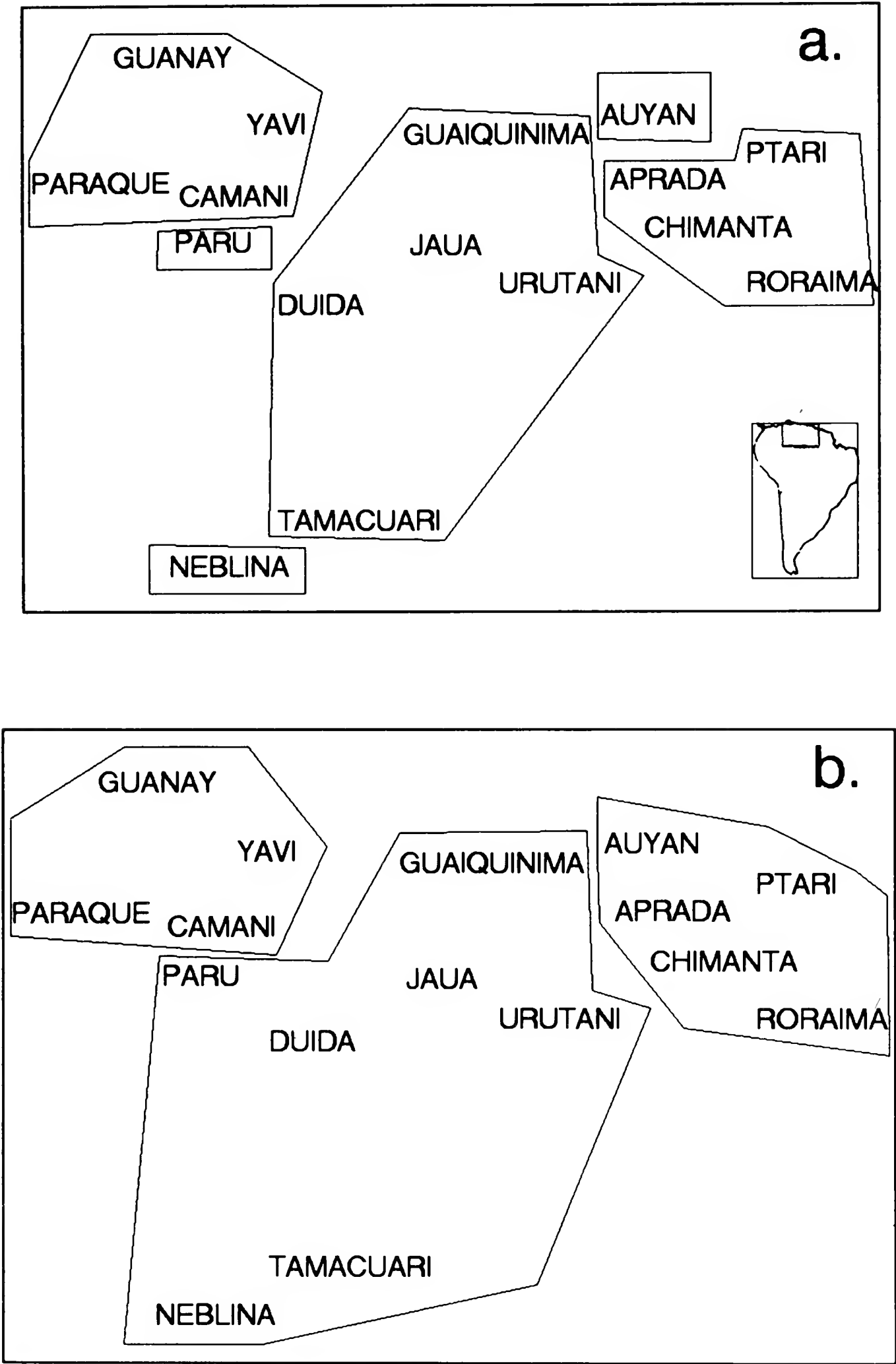


FIGURE 2 – Patterns of geographic variation in the Tepui Brush-Finch complex in the pantepui region of Venezuela; approximate geographic configuration of tepuis is depicted by position of names on diagram. a: geographic distributions of the six currently recognized subspecies are indicated by circumscribed tepuis. b: geographic pattern of three homogeneous regions computed using SS-STP analysis of specimen measurements.

VARIATION IN THE TEPUI BRUSH-FINCH

The Tepui Brush-Finch *Atlapetes personatus* occurs in subtropical vegetation and brush above approximately 1000 meters on the tepuis of Venezuela. These birds have a discontinuous, island-like geographical range due to the disjunct distribution of their requisite habitat. Over the years, six subspecies have come to be recognized (Figure 2a); some of these were based on pronounced differences in plumage pattern among populations, but other subspecies reflected quite subtle differences in color based on small sample sizes. In the course of investigating geographic variation in this species (Barrowclough 1991a), I measured a number of characters on museum skins. Some of the characters reflected features, such as amount and shade of red on the throat, used in describing the recognized races; however, other characters were traditional measurements, such as culmen and wing length, not mentioned in those descriptions.

Analyses of the univariate characters using SS-STP indicated a general pattern, over several of the characters, of organization of the various tepuis into three discrete regions. These regions did not conflict with any of the recognized subspecies, but the races did tend to overshadow the pattern "found" by the SS-STP (Figure 2b). That is, three single populations, each described as a subspecies on the basis of subtle differences in color, are equivalent in rank to three races reflecting major plumage pattern differences; this mixture of levels of differentiation obscures the actual hierarchy of the three regions. In a sense, then, there are two competing patterns available to describe geographic variation in the Tepui Brush-Finch — three equally ranked regions or six equally ranked races. Variance partitioning provides a method for judging the efficacy of these two patterns through estimating the magnitude of variance they explain.

Three different analyses were used in evaluating the alternate patterns of geographic variation. In the first, an ANOVA was performed with a single hierarchical level, the population. For culmen length, for example, 53% of the variance was among populations, and 47% within. In a two level analysis, based on the six described subspecies, 38% of the variance was among subspecies, 20% among populations within subspecies, and 42% within populations. Lastly, in a second two level analysis, the six subspecies were replaced by the three regions; here 47% of the variance was among regions, 13% among populations within regions, and 40% within populations. That is, the three regions explained considerably more of the variation than did the six subspecies. The greater explanatory power of the regions, in terms of magnitude of variance partitioned, was true of five of the six characters examined, and this ignores the fact that the regions involve only two degrees of freedom versus the five for the races. Here the estimation of the quantity of variation associated with various patterns offered a method for evaluating the alternatives.

FUTURE INVESTIGATIONS

The nested ANOVAs in the above examples provide a technique that may further the development of comparison in avian studies of geographic variation. However, problems remain that require investigation. Of immediate interest are inquiries into, first, statistical matters concerning the robustness of the results to limitations of data typically available for birds, and, second, the nature of comparisons involving unknown,

but probably differing, genetic and epigenetic bases. In the first category, one should round up the usual suspects when it comes to ANOVA: the statistical distribution of the original measurements and the residuals, the balance of the design, the proper model, etc. For example, the use of ranks may be appropriate when there are questions about the distribution of the original scores; examination of results using subsets of the data may be helpful with unbalanced sample sizes and numbers of levels in nested ANOVAs; and using separate analyses on males and females may help to avoid the mixing of fixed and random effects. Also of concern is the stability of the results to sampling variation; some bootstrapping might be useful in this regard. In the second category there is the problem of making comparisons between traits with varying genetic components (e.g., James 1983). For example, in some instances it may make sense to compare patterns of Mendelian traits with others having low heritability and unknown environmental influences. However, in other cases such comparisons would be misleading: for example, if one were making inferences concerning process rather than pattern. Comparisons of traits across species will frequently involve unknown genetic architectures.

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POPULATION DIFFERENTIATION IN COLONIZING SPECIES OF BIRDS

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ABSTRACT. To elucidate patterns and processes of population differentiation in colonizing birds, we compared ancestral populations of House Sparrows, Starlings, Chaffinches and Common Mynas with their descendent populations originally introduced to New Zealand last century. Genetic and morphometric shifts between ancestral and descendent populations are generally small, but they nevertheless mostly equal levels of population differentiation in connected ancestral demes. Rate tests indicate that these differences can be accounted for by random drift in the new isolates. Gene flow among localities in New Zealand is apparently not sufficient to prevent stochastic differentiation, especially in Starlings and Chaffinches. In House Sparrows and Common Mynas, the trend of increasing size in warmer northern localities in New Zealand may indicate selection for optimal body size, but environmental induction cannot be ruled out until the requisite field experiments are performed.

Keywords: Population differentiation, morphometrics, genetic variation, colonizing species.

INTRODUCTION

In 1965 a symposium entitled "The genetics of colonizing species" was published in the Proceedings of the First International Union of Biological Sciences in General Biology. An important paper in this symposium was one by Ernst Mayr on the nature of colonizations in birds. At that time he noted that ornithologists could make only an indirect contribution to the central theme of the symposium. However, he argued they could contribute much to phenotypic changes observed in birds whose colonizing histories were well known, and thus inferences could be made about underlying genetic changes in these species.

As noted by Barrowclough in the previous paper in this symposium, around this time researchers in the field of population differentiation began utilizing powerful new tools of multivariate statistical analysis and protein electrophoresis to gain more detailed information on phenotypic and genetic changes occurring in colonizing species of birds (e.g. Power 1971, Johnston & Selander 1971, 1973, Baker 1980, Ross & Baker 1982, Ross 1983, Baker & Moeed 1979, 1987, Baker et al. 1990a, b, Fleischer et al. 1991). These sophisticated analyses did not initially allow researchers to journey beyond narrative explanations of local adaptation of populations, the cornerstone of neo-Darwinian microevolutionary theory.

Recently, however, biologists have become increasingly interested in employing null hypotheses of phenotypic and genetic divergence of populations predicated on neutral theory (e.g. Barrowclough et al. 1985, Lynch & Hill 1986, Turelli et al. 1988, Lynch 1988). Rejection of these null hypotheses then argues strongly for an adaptive basis to population differentiation, although the reverse is not necessarily true.

In this paper we summarize some of the important advances in our thinking about population differentiation in colonizing species of birds since the 1965 symposium.

Colonizing species have been intensively studied in the intervening 25 year period because each provides a fortuitous replicated, natural "experiment" in which we can record the magnitude, pattern, and rate of population divergence in the descendent populations relative to their known ancestral stock. Rather than providing a compilation and synthesis of all studies conducted on birds, we will instead focus on four species of passerines (the Chaffinch *Fringilla coelebs*, House Sparrow *Passer domesticus*, Common Myna *Acridotheres tristis*, and European Starling *Sturnus vulgaris*) that have been very successful colonizers in various parts of the world, most notably in the host country for the XXth International Ornithological Congress, New Zealand. All four species were introduced into New Zealand last century. Founder population sizes were approximately 70 for Common Mynas, 110 for House Sparrows, 400 for Chaffinches, and at least 500 for Starlings.

MATERIALS AND METHODS

Details of the population samples of the four species of colonizing passerines used in this study are provided in previous publications (Baker & Moeed 1979, 1980, 1987, Baker 1980, Ross & Baker 1982, Ross 1983, Gibson et al. 1984, Baker et al. 1990a). Both morphometric and genetic data for ancestral and descendent populations were gathered from the same specimens of each species, with the exception of House Sparrows. For the latter, all genetic data were taken from Parkin & Cole (1985), and morphometric data for English populations of this species were measured on three of the seven populations electrophoresed by these authors.

The magnitude of among-population differentiation was assessed separately in the ancestral and descendent populations. Because the geographic scale of sampling was not equivalent for all species, we used both univariate added variance components from ANOVA of skeletal characters as well as multivariate average taxonomic distances (d ; Sneath & Sokal 1973) to quantify morphometric differentiation. The latter are less sensitive to the scale of sampling because of the pairwise computation of these differences. To make the variances of the skeletal characters independent of their respective means, they were \ln -transformed before the calculation of variance-covariance matrices computed among population means. The pattern and magnitude of differentiation was then displayed by projecting the population means onto the first two principal components.

Genetic differentiation in each of the four species was compared using the number of geographically variable loci detected with contingency chi-square tests ($P < 0.01$), as well as F_{ST} the portion of the genetic variance distributed among populations. Multilocus differentiation was computed using Rogers' (1972) genetic distance because of its metric properties, and the pattern of divergence was displayed using a two-dimensional principal coordinates analysis of these distances. To indicate possible distortions in the placement of populations in the reduced 2-D space, a minimum spanning tree (MST) was fitted among the population centroids to show their full-dimensional relationships.

Under the assumption that the divergence of the means of morphometric characters of descendent New Zealand populations from their ancestral stock are genetically based, it is possible to employ a test of evolutionary rates expected under simple

neutral models. Because the timeframe since the introduction of the four species into New Zealand is too short (< 130 years) for the establishment of mutation-drift equilibrium, it is most appropriate to use Lande's (1976) constant heritability analysis (Turelli et al. 1988). The hypothesis under test with Lande's model is that the change in the mean phenotype for a particular character in a single population is caused by random drift of effectively neutral characters.

With Lande's (1976) rate test, drift can be rejected at the 5% level as the cause of divergence of mean phenotypes over $t = 130$ generations if

$$N_e > N_e^* = \frac{(1.96)^2 h^2 t}{\left(\frac{z}{\sigma}\right)^2}$$

where h^2 is the heritability of the trait under study, z is the difference in mean phenotypes, σ is the standard deviation of the trait, and N_e is the effective size of the colonizing population. For morphometric characters of birds, heritabilities typically range between 60% and 70%, and we have used the lower figure to produce a conservative estimate of N_e^* . To obtain a representative estimate of σ for the four species, pooled standard deviations were computed separately for each species over all New Zealand populations.

DIVERGENCE OF DESCENDENT AND ANCESTRAL POPULATIONS

Morphometric divergence

The magnitude of morphometric divergence of New Zealand descendent populations of Chaffinches, House Sparrows, and Starlings from their English 'ancestral' populations is relatively small. Deviations of means of skeletal morphometric characters between descendent populations and their most similar ancestral populations average 0.81%, 1.44%, and 0.73% respectively for the three species. New Zealand populations of Common Mynas, however, have diverged more noticeably from their Indian ancestral stock, the average divergence for skeletal morphometric characters being 1.77%. Unlike the other species, the descendent New Zealand populations of Common Mynas are smaller than their most similar ancestral population in all skeletal characters (Calcutta). In Chaffinches, the New Zealand populations are on average larger in all morphometric characters except lengths of leg bones, in which they are smaller than their morphometrically closest English population (Wareham). Similarly, the New Zealand populations of House Sparrows and Starlings are also on average larger than their most similar United Kingdom population (Nottingham) in most skeletal characters.

The magnitude of morphometric divergence between ancestral and descendent populations can best be appreciated multivariately using plots of the first two principal components (Figure 1). For all four species divergence has occurred mainly in general size (PC I), though some shape changes have also occurred (PC II). The divergence of Common Mynas in general size is especially evident, and this includes the extant population in Melbourne, Australia, from which the New Zealand populations were derived about 10 years after the initial introduction of birds from

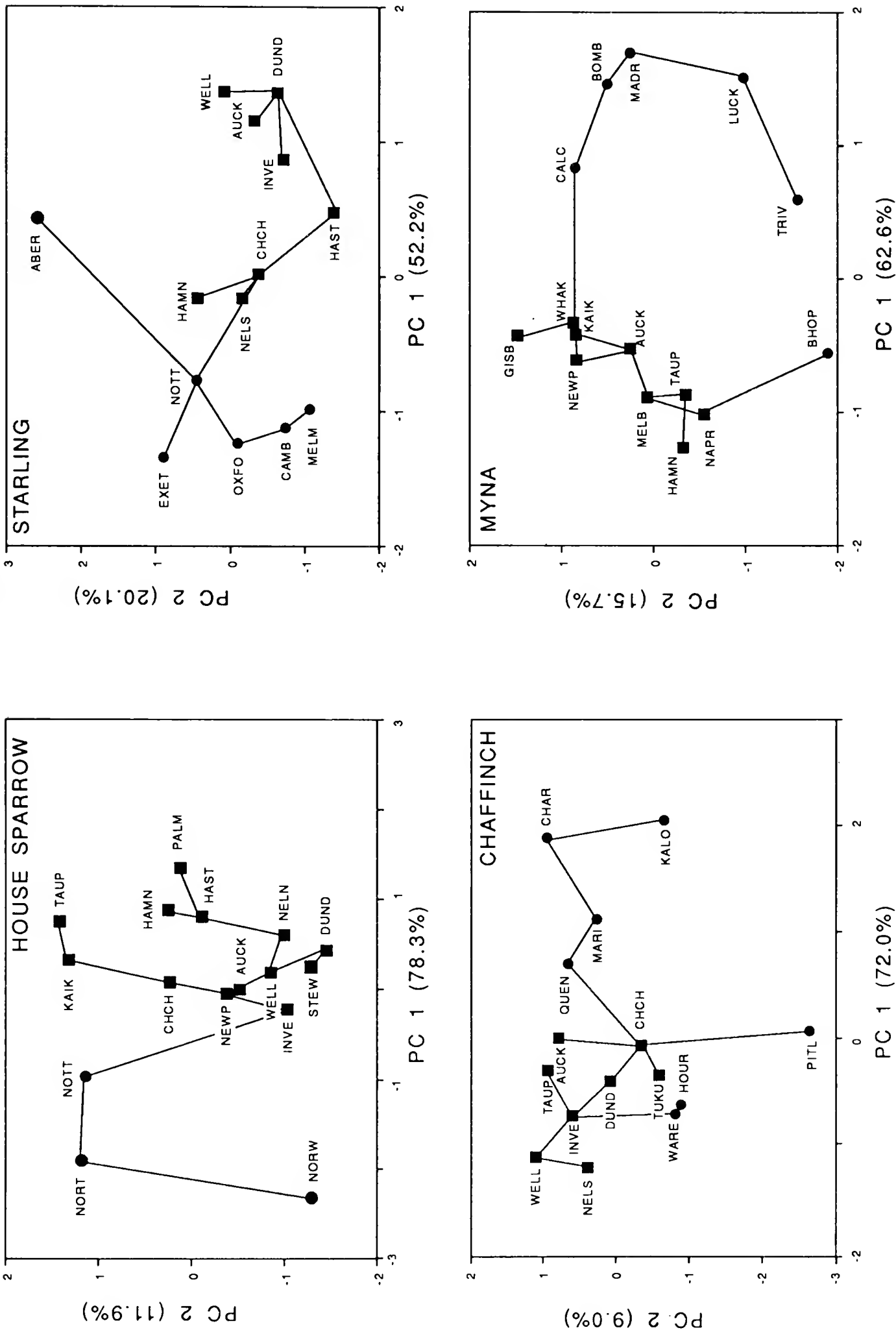


FIGURE 1 - Principal component plots of morphometric variation in skeletal characters of four colonizing species of passerines. Population centroids are connected by a minimum spanning tree of average taxonomic distances. Ancestral populations are denoted with solid circles and descendent populations with solid squares.

India to Melbourne in 1862. Although ancestral and descendent populations of Starlings have diverged in general size, the Nelson sample in central New Zealand is morphometrically very similar to its United Kingdom counterparts. The New Zealand populations of Chaffinches are very similar in size to the two United Kingdom samples, especially the sample from Wareham in southern England, where at least some of the transplanted birds were taken (Ince et al. 1980). The larger multivariate size of New Zealand populations of House Sparrows relative to northeast English populations from around Norwich and Nottingham is also clearly depicted in Figure 1.

Rate tests of the divergence of the morphometric means of the New Zealand descendent populations from their most similar ancestral population for each species revealed that the hypothesis of random drift of essentially neutral characters cannot be rejected as the cause of their divergence. For House Sparrows, Chaffinches, and even the more divergent Common Mynas, all skeletal characters yield estimates of $N_e^* \gg N_e$ in the founder populations. In Starlings, one character out of 14 (cranium depth) has $N_e^* < N_e$, and another (premaxilla length) approaches the boundary estimate. Thus for these two characters the divergence of the descendent populations from the ancestral populations appears to be too great to be accounted for solely by drift.

Genetic divergence

The genetic divergence of ancestral and descendent populations of the four species of colonizing passerines is summarized in Table 1 for the number of loci showing significant geographic variation, the among population component of genetic variance (F_{st}), and mean Rogers' genetic distance (D_R). For all species, the establishment of colonizing populations in New Zealand has led to an increase in the average among-population genetic distances. Relative to the ancestral populations, levels of genetic subdivision (as judged by F_{st} values) in each species have also increased due to the divergence of the colonizing populations in New Zealand. The greater morphometric divergence of ancestral and descendent populations of Common Mynas compared to the other three passerines is paralleled by correspondingly greater genetic divergence in this species (Table 1).

TABLE 1 - Morphometric and genetic divergence within and among ancestral and descendent populations of four colonizing species of birds.

Species	Comparison	Morphometrics			Genetics		
		N ^a	V _a	d	N ^b	F _{st}	D _R
House Sparrow	N.Z. & England ^c	8	6.2	0.034	8	0.015	0.026
	Within N.Z.	11	5.3	0.013	4	0.005	0.020
	Within England	6	6.9	0.019	3	0.010	0.021
Starling	N.Z. & U.K. ^d	9	5.1	0.013	6	0.038	0.025
	Within N.Z.	5	3.1	0.009	6	0.032	0.019
	Within U.K.	9	4.1	0.011	1	0.010	0.008
Chaffinch	N.Z. & U.K. ^e	1	2.3	0.013	9	0.034	0.031
	Within N.Z.	2	2.8	0.010	6	0.040	0.026
	Within U.K.	2	6.4	0.014	1	0.006	0.016
Common Myna	N.Z. & India ^f	11	22.2	0.022	18	0.059	0.035
	Within N.Z.	10	5.3	0.011	4	0.016	0.105
	Within India	13	30.8	0.021	2	0.032	0.023

^a Number of geographically variable characters. ^b Number of geographically variable loci. ^c Seven localities in northeastern England (Parkin & Cole 1985). ^d Six localities in England and Scotland (Ross 1983). ^e One locality in England and one in Scotland, ^f Six localities in India.

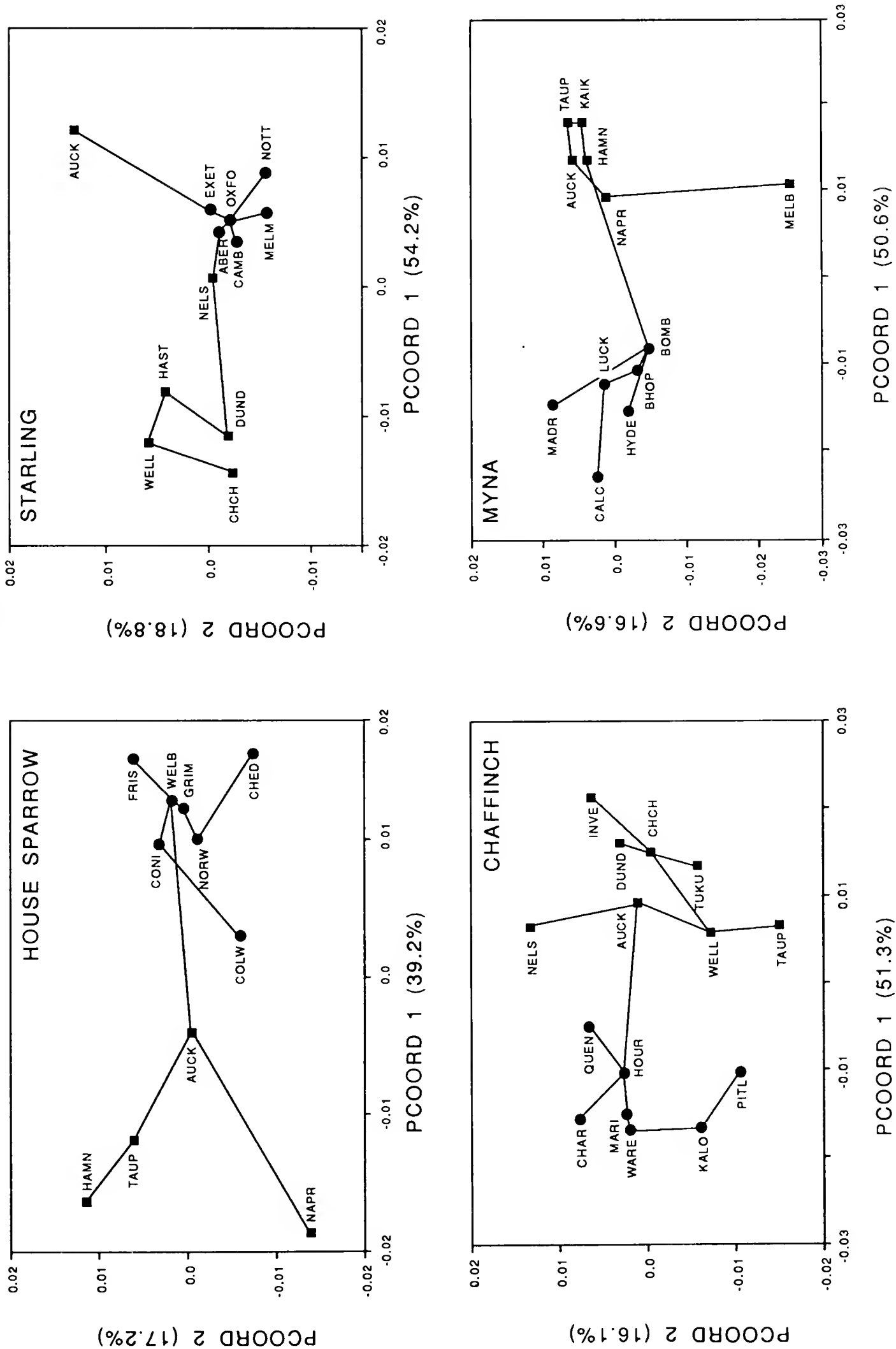


FIGURE 2 - Principal coordinate plots of genetic differentiation among ancestral and descendent populations of four species of colonizing passerines. Population centroids are connected by a minimum spanning tree of Rogers' (1972) genetic distances. Ancestral populations are denoted with solid circles and descendent populations with solid squares.

Multilocus graphic representations of the genetic divergence of ancestral and descendent populations are provided by the principal coordinates plots for each species in Figure 2. These plots clearly indicate that the descendent populations are genetically differentiated from their ancestral counterparts in all species, with the exception that the Nelson sample of Starlings groups closely with the United Kingdom samples. Interestingly, in Common Mynas, the most genetically divergent sample is the one from Melbourne, indicating that this population has diverged at a faster rate than the derivative New Zealand populations.

POPULATION DIFFERENTIATION IN COLONIZING POPULATIONS IN NEW ZEALAND

Morphometrics

The magnitude of population differentiation in morphometric characters among colonizing populations of House Sparrows and Starlings is similar to that in the ancestral populations from which they are derived (Table 1). However, ancestral populations of Chaffinches and Common Mynas are more differentiated than their respective descendent populations in New Zealand. In Common Mynas, average taxonomic distances among populations in India are about double those in New Zealand, and in House Sparrows they are about 50% larger in the northeast England populations to those over the whole of New Zealand.

There are clear differences among species in the degree of geographic variation they have developed. In particular, Chaffinches and Starlings are much less differentiated morphometrically among populations than are the other two species. House Sparrows and Common Mynas have differentiated significantly within New Zealand in more than half the 14 skeletal characters measured in this study, whereas Chaffinches and Starlings have only developed significant geographic variation in two and five characters, respectively. In New Zealand, the average added variance component (V_A) of individual characters, the portion of the total morphometric variance partitioned among localities, is only about half as large in Chaffinches and Starlings as in the other species (Table 1).

Genetics

At the level of apparently neutral allozyme loci, population differentiation is qualitatively different to that in morphometric characters. For Starlings, Chaffinches, and Common Mynas, statistically significant heterogeneity in allele frequencies was detected at twice or more the number of loci in the New Zealand populations than in their ancestral counterparts (contingency χ^2 tests, $P < 0.01$). In House Sparrows, however, similar numbers of geographically variable loci were found in ancestral and descendent populations, though in both New Zealand and the United Kingdom only a restricted part of the total ranges were sampled.

Genetic structuring is only weakly developed in ancestral and descendent populations in all four species. In both Starlings and Chaffinches, values of F_{st} are lower in the ancestral populations in the United Kingdom (Table 1). For Common Mynas and House Sparrows the situation is reversed, with the ancestral populations having higher F_{st} values. Multilocus genetic distances show the same pattern of population

differentiation, with the exception that ancestral and descendent populations of House Sparrows are about equally differentiated (Table 1).

DISCUSSION

Processes of population differentiation in colonizing species

The four species of passerine birds studied here have successfully colonized a range of habitats in New Zealand in about 100-130 years since their introduction last century. In this short period of time, small scale population differentiation in morphometric characters of the skeleton and in protein-encoding nuclear genes has developed in this novel environment. The genetic and morphometric shifts that these colonizing populations have undergone relative to their ancestral stock are also quite small, but nevertheless they are mostly about equal or exceed in magnitude the levels of population differentiation that have presumably developed over many millenia in connected continental demes.

Exploratory rate tests of the divergence of means of morphometric characters in all four species cannot reject the null hypothesis of random drift as the cause of this divergence, even in Common Mynas where all characters are smaller in descendent populations in New Zealand. Although these tests do not definitively rule out a role for natural selection in the divergence of ancestral and descendent populations, it is clear that extremely small selection coefficients would be involved and thus characters would be effectively neutral or nearly so (Baker et al. 1990a). This conclusion highlights the conceptual advances in our thinking about microevolutionary diversification of populations that have occurred since Mayr's 1965 paper on colonizing species of birds. Adaptive narrative explanations, so characteristic of this earlier period when the new synthetic theory was dominating evolutionary biology, are no longer accepted in lieu of more compelling supporting evidence for causal mechanisms.

Earlier analyses of population differentiation in New Zealand populations of House Sparrows showed that size variation was ordered approximately clinally, with birds averaging larger in warmer northern localities. Because this variation in size was associated with an essentially N-S climatic gradient, and because the sexes have responded differently to environmental variation, it was argued that natural selection for ecoclimatic adaptation was occurring in the New Zealand populations (Baker 1980). A similar argument was also advanced by Johnston & Selander (1971, 1973) to explain the continental scale of geographic differentiation in North American populations of House Sparrows. New Zealand populations of Common Mynas show the same tendency as House Sparrows to be larger in northern localities (Baker & Moeed, 1979). Conversely, populations of Starlings and Chaffinches show no such trend, and instead morphometric variation among localities is haphazard with respect to environmental gradients (Ross & Baker 1982, Baker et al. 1990a).

Geographic surveys of allele frequencies in allozymes were undertaken to directly reveal underlying patterns of genetic differentiation, rather than relying on inferences about genetic changes based on morphometric characters. These studies revealed that genetic drift has played an important role in population differentiation, and therefore implied that gene flow among localities in New Zealand is not sufficient to overcome stochastic differentiation, at least in Starlings and Chaffinches (Ross 1983,

Baker et al. 1990a). Geographic subdivision of the New Zealand landmass by water barriers, mountains, and native forests that are almost impenetrable for these passerines have apparently limited gene flow much as in native species (see companion paper in this symposium by Daugherty and Triggs). This finding raises the question of whether the N-S trend of increasing size in House Sparrows and Common Mynas in New Zealand is really ordered by natural selection for climatic adaptation, especially since it is the reverse of that predicted by Bergmann's rule. An alternative explanation is that these body size trends are wholly or partly environmentally induced, as has been demonstrated in Red-winged Blackbirds *Agelaius phoeniceus* by James (1983). Transfer experiments among localities in New Zealand with different climates are urgently needed to test this hypothesis. The realization that a large environmental component in birds can be misinterpreted as selection for local adaptation is another important conceptual advance since the 1965 symposium.

The different patterns of population differentiation in New Zealand by Chaffinches and Starlings on the one hand, and House Sparrows and Common Mynas on the other, almost certainly implicate agencies other than climatic ones. Future studies need to address morphological responses to niche width, food particle size, and the depauperate matrix of competitor species encountered by colonizing species in New Zealand relative to ecological conditions in their ancestral communities. Ecological variation potentially can be a potent force in population differentiation via selection for optimal body size (Case 1978). Finally, more attention needs to be focussed on the possible role of ecological and sexual selection on body size of males in colonizing species in New Zealand, since it is now well established that males have developed greater levels of population differentiation than have females in all four species thus far studied. As noted by Baker (1980), New Zealand provides a wonderful natural laboratory in which to conduct such important studies.

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MITOCHONDRIAL DNA AND AVIAN MICROEVOLUTION

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ABSTRACT. Mitochondrial (mt) DNA provides a rich source of uniparentally-transmitted genetic markers especially useful in the study of matriarchal phylogeny over microevolutionary timescales. Various applications of mtDNA data to avian taxa are reviewed, including the assessment of: (1) magnitudes of intraspecific polymorphism; (2) genetic distinctions between sibling species; and (3) genetic distances and phylogenies among congeners. Special attention is focused on patterns of geographic differentiation within avian species, where conspecific populations have proved to exhibit a variety of mtDNA phylogeographic structures. The deep and geographically structured subdivisions observed in the mtDNA genealogies of some avian species probably evidence the effects of Pleistocene biogeographic separations, while the additional, shallower mtDNA subdivisions and haplotype frequency shifts distinguishing populations of most species probably reflect more recent restrictions on gene flow. In general, mtDNA data offer a novel, phylogenetic perspective on microevolutionary processes, and allow provisional interpretation of contemporary population structure in terms of historical demography.

Keywords: Mitochondrial DNA, phylogeography, population structure, genetic markers, gene flow, historical demography.

INTRODUCTION

Because of its rapid evolution and uniparental inheritance, mitochondrial (mt) DNA offers novel perspectives on microevolutionary processes in higher animals (Avise et al. 1987, Wilson et al. 1985). A major motivation for mtDNA surveys of birds has been the need for critical reassessment of the processes governing genetic differentiation among conspecific populations. Few topics have generated greater discussion in recent years, yet there remain conflicting opinions on the magnitude of contemporary gene flow and historical connectedness among avian populations. On the one hand, most birds have high dispersal potential (because of flight), and many species have broad geographic distributions, suggesting that gene flow is high and population differentiation minimal. On the other hand, many species exhibit strong tendencies for nest-site philopatry (Greenwood 1980), and commonly show obvious geographic variation in size, song, or plumage (often leading to the description of subspecies), suggesting that inter-population gene flow is normally quite low. But since the genetic bases and evolutionary forces governing most morphological or behavioral differences are poorly understood, their relevance to estimating gene flow and magnitude of genetic divergence is unclear. Clearly, a reappraisal of avian population structure that capitalizes on the resolving power of mtDNA, and the historical perspective it provides, is appropriate.

BACKGROUND, AND CALIBRATION OF MTDNA EVOLUTION IN BIRDS

Presumably, mtDNA inheritance is predominantly or exclusively maternal in birds, as in most other multicellular animals (Avise & Vrijenhoek 1987). However, only a single direct test of avian mtDNA transmission appears available: Watanabe et al. (1985)

showed that progeny of a cross between a female Japanese quail and a male chicken exhibited the mtDNA genotype of the mother.

Glaus et al. (1980) and Shields & Helm-Bychowski (1988) review evidence that the molecular features of avian mtDNA variation are similar to those of other vertebrate classes. Thus the molecule is about 16-20 kilobase-pairs in length, evolves primarily through nucleotide substitutions, and is normally homoplasmic (occurs as a single predominant genotype within an individual — but see Avise & Zink 1988). The complete sequence of one avian mtDNA recently has been obtained (Desjardins & Morais 1990). In comparison to mammals and the clawed frog, whose mtDNAs are identical in gene content and order, chicken mtDNA lacks sequences associated with the light-strand replication origin, and exhibits a transposition of two loci.

Only two explicit tests of mtDNA evolutionary rate appear available for birds. First, based on her own mtDNA data and those of Glaus et al. (1980), Helm-Bychowski (1984) plotted an initial rate of about 2% sequence divergence per million years between several Galliforme species. Second, Shields & Wilson (1987) observed about 9% sequence divergence between *Anser* and *Branta* geese that from fossil evidence last shared a common ancestor about 4-5 million years ago. Both studies thus yielded evolutionary rate estimates close to the conventional mtDNA “clock” calibration for non-avian vertebrates (Brown et al. 1979).

The rapid pace of mtDNA evolution has raised hope that the molecule can provide a rich source of genetic markers for closely related avian species (some of which are difficult to distinguish by morphological or allozyme traits). Initial results, summarized in Table 1, indicate that many fixed restriction site differences do indeed distinguish some sibling taxa of birds.

TABLE 1 - Genetic differences between avian sibling taxa observed in conventional surveys of allozymes and mtDNA. Data for the first four comparisons come from Avise & Zink (1988); those for the other *Parus* from Braun & Robbins (1986; allozymes) and Mack et al. (1986; mtDNA); *Ficedula*, Gelter (1989).

Taxon pair	No. characters surveyed		No. fixed differences		Genetic distance	
	allozyme loci	mtDNA sites	allozyme alleles	mtDNA sites ^a	allozyme <i>D</i> ^b	mtDNA <i>p</i>
<i>Rallus elegans</i> v <i>R. longirostris</i>	38	68	0	5	0.004	0.006
<i>Limnodromus scolopaceus</i> v <i>L. griseus</i>	36	77	2	24	0.060	0.082
<i>Quiscalis major</i> v <i>Q. mexicanus</i>	38	80	0	10	0.001	0.016
<i>Parus bicolor bicolor</i> v <i>P.b. atriscristatus</i>	36	83	0	5	0.063	0.004
<i>Parus atricapillus</i> v <i>P. carolinensis</i>	35	80	0	17	0.001	0.040
<i>Ficedule hypoleuca</i> v <i>F. albicollis</i>	35	214	0	>8	0.001	0.010

^a Conservative estimate, assuming that fragment profile differences not due to a single restriction site gain/loss are due to only two such changes.
^b Nei's (1978) distance measure.

In a few cases, closely related species could *not* be separated cleanly on the basis of mtDNA genotype. For example, two genetically distinct arrays of mtDNA haplotypes were present in Mallard *Anas platyrhynchos* populations, while only one of these arrays was represented among the assayed Black Ducks *A. rubripes* (Awise et al. 1990). One possibility is that the distinct mtDNA genotypes were transferred between species via secondary hybridization. Alternatively, the phylogenetic split in the mtDNA gene tree may have predated the speciation event, such that the Mallard-Black complex now exhibits a "paraphyletic" relationship in terms of mtDNA genealogy.

Table 2 summarizes mtDNA genetic distances between non-sibling avian congeners. Levels of sequence divergence range between 0.4 and 11%. Most such estimates of avian mtDNA sequence divergence are considerably lower than mean values for other vertebrate genera such as *Lepomis* sunfish and *Hyla* treefrogs, and thus parallel the conservative pattern of divergence in avian allozymes relative to these non-avian taxa (Kessler & Awise 1985). However, some non-avian vertebrate genera exhibit means and ranges of mtDNA *p* quite comparable to those reported for birds (review in Shields & Helm-Bychowski 1988).

MtDNA distances among avian congeners are well within the expected linear portion of a curve relating sequence divergence to time (Brown et al. 1979). Thus the mtDNA distances may be of considerable utility in estimating phylogeny among closely related avian species, a suggestion strongly supported by the results of three multi-species systematic studies. Within *Anas* and *Aythya* ducks (Kessler & Awise 1984), *Platycercus* rosellas (Ovenden et al. 1987), and *Ammodramus* sparrows (Zink & Awise 1990), phylogenies inferred from mtDNA data agree well with those based on independent sources of genetic and/or other biological information.

Levels of mtDNA polymorphism within avian species are usually high (Table 3). In a typical survey involving about 100 restriction sites scored per organism, a random pair of conspecific individuals differs detectably in mtDNA genotype with probability 0.70 or higher (genotypic diversity), and exhibits a sequence divergence (nucleotide diversity) of about 0.3%. Nonetheless, mtDNA polymorphism remains far lower than predicted under neutrality theory, given suspected rates of sequence divergence and current day population sizes (Awise et al. 1988). For example, Figure 1 plots the observed and expected times to common mtDNA ancestry in the Red-winged Blackbird (*Agelaius phoeniceus*). The observed mean distance between mtDNA lineages is more than two orders of magnitude lower than might have been anticipated from the census size of breeding females. Either the rate of mtDNA evolution is decelerated in such species, and/or evolutionary effective population sizes are vastly smaller than present-day population sizes. In principle, the latter could result from historical fluctuations in female numbers, or from a periodic positive directional selection on mtDNA genotypes that would have a similar net effect of channeling mtDNA through fewer female ancestors (Awise 1989).

PHYLOGEOGRAPHIC DIFFERENTIATION WITHIN AVIAN SPECIES

Because the phylogenies of haplotypes can be inferred from mtDNA data, considerations of historical as well as contemporary aspects of population structure are possible. A straightforward method for summarizing the information content of mtDNA

TABLE 2 - Genetic distances in mtDNA (*p*, base substitutions per nucleotide) reported for comparisons between avian congeners.

Genus	No. pairwise species comparisons	No. endonucleases employed	No. sites scored per individual	mtDNA <i>p</i>	reference
Passeriformes					
<i>Dendroica</i>	10	17	71	0.031-0.055	Kessler & Avise 1985
<i>Melospiza</i>	3	18	59	0.026-0.030	Kessler & Avise 1985
<i>Ammodramus</i>	28	16	67	0.021-0.109	Zink & Avise 1990
<i>Parus</i>	3	14	39	0.04-0.09	Mack et al. 1986
non-Passeriformes					
<i>Anas</i>	36	15	54	0.004-0.088	Kessler & Avise 1984
<i>Aythya</i>	6	15	54	0.025-0.043	Kessler & Avise 1984
<i>Branta</i>	1	14	75	0.061	Shields & Wilson 1987
<i>Anser</i>	2	14	75	0.027-0.028	Shields & Wilson 1987
<i>Platycercus</i>	15	6	≈156	0.017-0.064	Ovenden et al. 1987

involves superimposing on a distributional map the genealogies inferred from the mutational differences among mtDNA haplotypes. The outcomes can then be classified into “phylogeographic” categories, interpreted against neutrality expectations, and compared among studies (Avise et al. 1987).

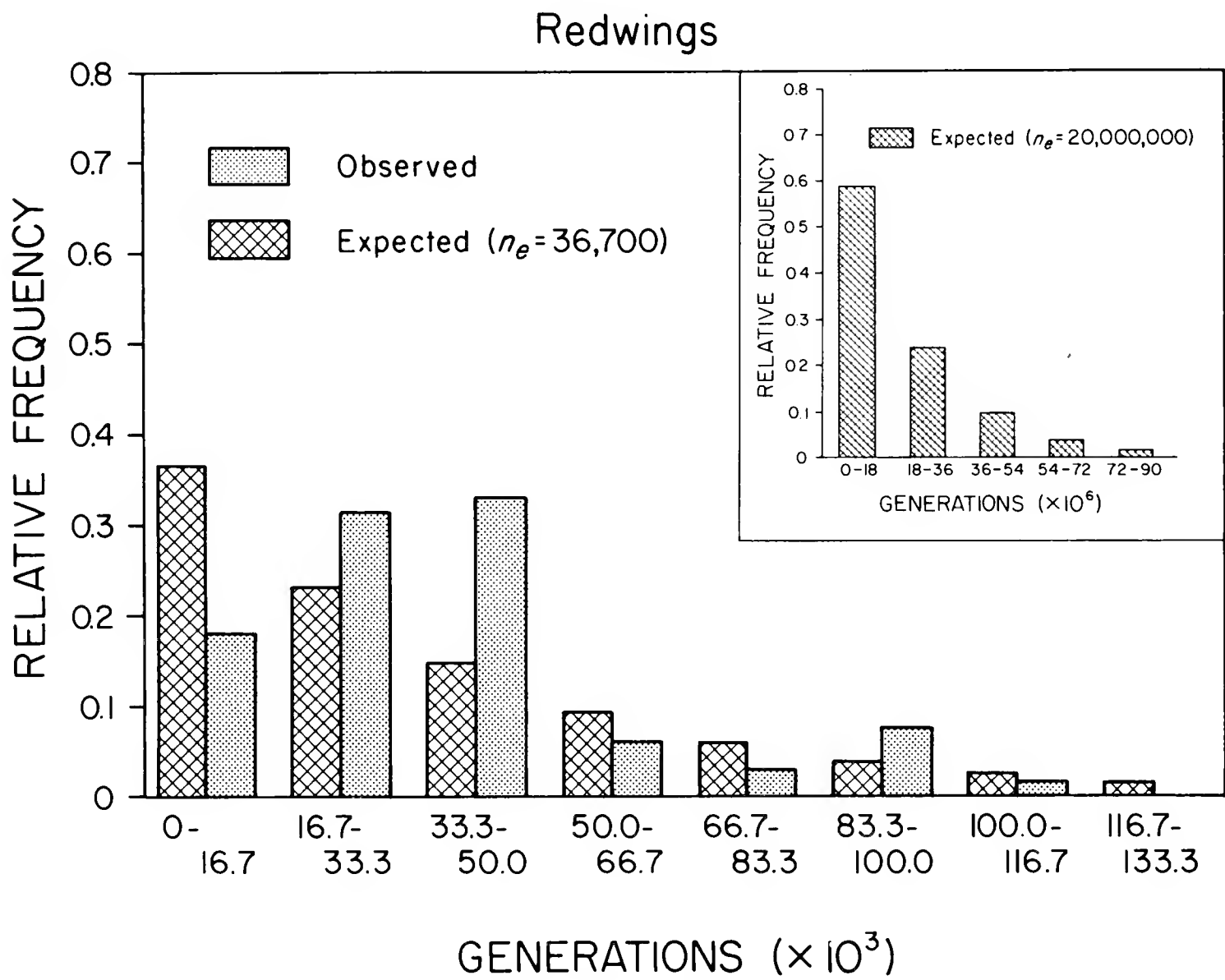


FIGURE 1 - Observed and expected frequency distributions of times to common ancestry for mtDNA haplotypes in the Red-winged Blackbird. Expected times generated from inbreeding theory (see text) are given for each of two conditions: 1) $N_{t(e)} = 20,000,000$ (a reasonable guess for the current breeding population of female redwings; shown in the inset); and 2) $N_{t(e)} = 36,700$ (a value which yields a mean expected divergence time equal to that inferred from the mtDNA data). Observed times were derived from the data of Ball et al. (1988), using a conventional mtDNA “clock” calibration and a generation length of three years. [Notice the difference in scale along the abscissas of the inset and main graph].

For example, genetic gaps (involving many mutational steps) might appear in the mtDNA phylogeny itself, and the clades thus identified could either be confined to particular geographic regions (phylogeographic category I) or broadly sympatric (category II). Alternatively, all mtDNA genotypes might be closely related, and particular haplotypes either geographically localized (category III), or widespread (category IV). If most avian populations have been connected historically by relatively high levels of gene flow (through high per-generation migration rates and/or periodic cycles of extinction and recolonization of local populations from a source), then most avian species should fall into phylogeographic categories II or IV, likely depending in part on whether the species-wide effective population sizes were large or small, respectively.

TABLE 3 - Estimates of mtDNA variability within species of birds for which sample sizes were greater than $n = 15$. Some values are provisional or approximate only, either because the studies were incomplete at the time of this writing, or because the data necessary for the calculations were not fully reported.

Species	Number of			genotypic nucleotide diversity ^a	geographic scale	reference
	inds.	different mtDNA genotypes	restriction sites or fragments per. ind.			
<i>Agelaius phoeniceus</i>	127	34	63	0.80	NA continent	Ball et al. 1988
<i>Ammodramus maritimus</i>	40	11	89	0.71	NY to LA	Avise & Nelson 1989
<i>Ammodramus caudacutus</i>	107	20	82	0.83	northern NA	Avise & Rising in prep.
<i>Parus major</i>	18	13	204	0.98	eastern Sweden	Tegelstrom 1987
<i>Passerella iliaca</i>	47	5	140	0.70	western US	Zink 1991
<i>Melospiza melodia</i>	27	10	96	0.85	western US	Zink 1991
<i>Picoides pubescens</i>	51	5	63	0.15	NA continent	Ball & Avise in prep.
<i>Branta canadensis</i>	53	11	183	0.71	northern NA	Van Wagner & Baker 1990
<i>Anas platyrhynchos</i>	20	7	93	0.80	western NA	Avise et al. 1990
<i>Anas rubripes</i>	20	3	93	0.49	eastern NA	Avise et al. 1990

^a genotypic diversity, $G = (n/n-1) (1 - \epsilon f_i^2)$, where f_i is the frequency of i th mtDNA haplotype in a sample of n individuals; and

^b nucleotide diversity, $p = (n/n-1) \epsilon f_i f_j p_{ij}$, where f_i and f_j are the frequencies of the i th and j th mtDNA haplotypes and p_{ij} is their estimated nucleotide sequence divergence.

Alternatively, severe restrictions on gene flow should result in patterns falling into phylogeographic categories I or III, depending on whether the restrictions were in force over long-term (evolutionary) versus short-term (ecological) timescales, respectively. Various intermediate situations may also exist. For example, ancestral mtDNA genotypes might be geographically widespread, while closely related, newly arisen mutations were localized (phylogeographic category V). One explanation for such an outcome might be that a species had expanded recently from a single refugium, but that its populations were currently experiencing limited genetic contact.

The following are brief synopses of the studies conducted to date on the mtDNA patterns observed in birds, as classified into the various phylogeographic categories of Avise et al. (1987).

Phylogeographic categories IV and V

The Red-winged Blackbird (*Agelaius phoeniceus*) was the first avian species assayed extensively in terms of mtDNA phylogeny (Ball et al. 1988). In a continent-wide survey involving 75 restriction sites and 127 individuals, 34 mtDNA clones were observed. Most genotypes were closely related (mean $p \approx 0.002$), and many of the mtDNA genotypes and clades were geographically widespread, suggesting considerable historical connectedness among populations, either through gene flow, and/or retention of genotypes from a recent ancestral population. On the other hand, some mtDNA genotypes and clades were rare or absent from particular regions, indicating a mild population structure. The evidence for this mtDNA structure is further supported by the form of the frequency distribution of haplotype distances, which departs significantly from the geometric distribution expected under the idealized "high gene flow" model (Figure 1).

One interpretation of the mtDNA data is that redwings recently colonized North America from a much smaller source population, perhaps since retreat of the last Pleistocene glacier some 13,000 years ago. If so, all redwing populations are closely related genetically, notwithstanding contemporary limits to dispersal and gene flow that allowed development of a mild genetic population structure across the continent. If this mtDNA-based scenario is correct, the extensive morphological differentiation among redwing populations (as reflected in the recognition of at least 23 subspecies) has occurred within the context of relatively shallow evolutionary separations. Perhaps some of the morphological differences are ecophenotypic [not based entirely on genetic differences, as is suggested by the nestling transplantation experiments of James (1983)]. Alternatively, genes responsible for morphological traits may have evolved so rapidly that geographic differentiation arose over a time-scale too short for clear detection by corresponding differences in the mtDNA assays.

Other avian species reported to exhibit phylogeographic category IV or V population structure include the Song Sparrow *Melospiza melodia* in the western U.S. (Zink 1991), and the Downy Woodpecker *Picoides pubescens* across North America (Ball & Avise in prep).

Phylogeographic category I

A survey of 40 Seaside Sparrows (*Ammodramus maritimus*) collected from New York to Louisiana revealed 11 mtDNA clones belonging to two distinct phylogenetic groups between which mean sequence divergence (after correction for within-group variation) was, $p \approx 0.01$ (Avise & Nelson 1989). One mtDNA array included all Atlantic coast

birds, while the other involved all Gulf coast specimens (Figure 2). This phylogeographic pattern probably evidences a long-term separation of Atlantic and Gulf coast populations, a scenario further supported by Funderburg & Quay's (1983) zoogeographic reconstruction for the species, and by the remarkable geographic concordance between the mtDNA partitions in the Seaside Sparrow and those of several other coastal species in the southeastern U.S. (Avisé & Ball 1990). The Atlantic-Gulf phylogenetic distinction in the Seaside Sparrow is not, however, recognized in the subspecies designations that provided the basis for population management decisions (Avisé & Nelson 1989).

Other avian species reported to exhibit a phylogeographic category I population structure include the Sharp-tailed Sparrow *Ammodramus caudacutus* (Avisé & Rising in prep), Fox Sparrow *Passerella iliaca* (Zink 1991), and Canada Goose *Branta canadensis* (Van Wagner & Baker 1990). In the latter species, two phylogenetically distinct mtDNA groups (differing by a mean sequence divergence of $p \approx 0.018$) were observed to correspond exactly to a subdivision of recognized subspecies into large-bodied versus small-bodied forms.

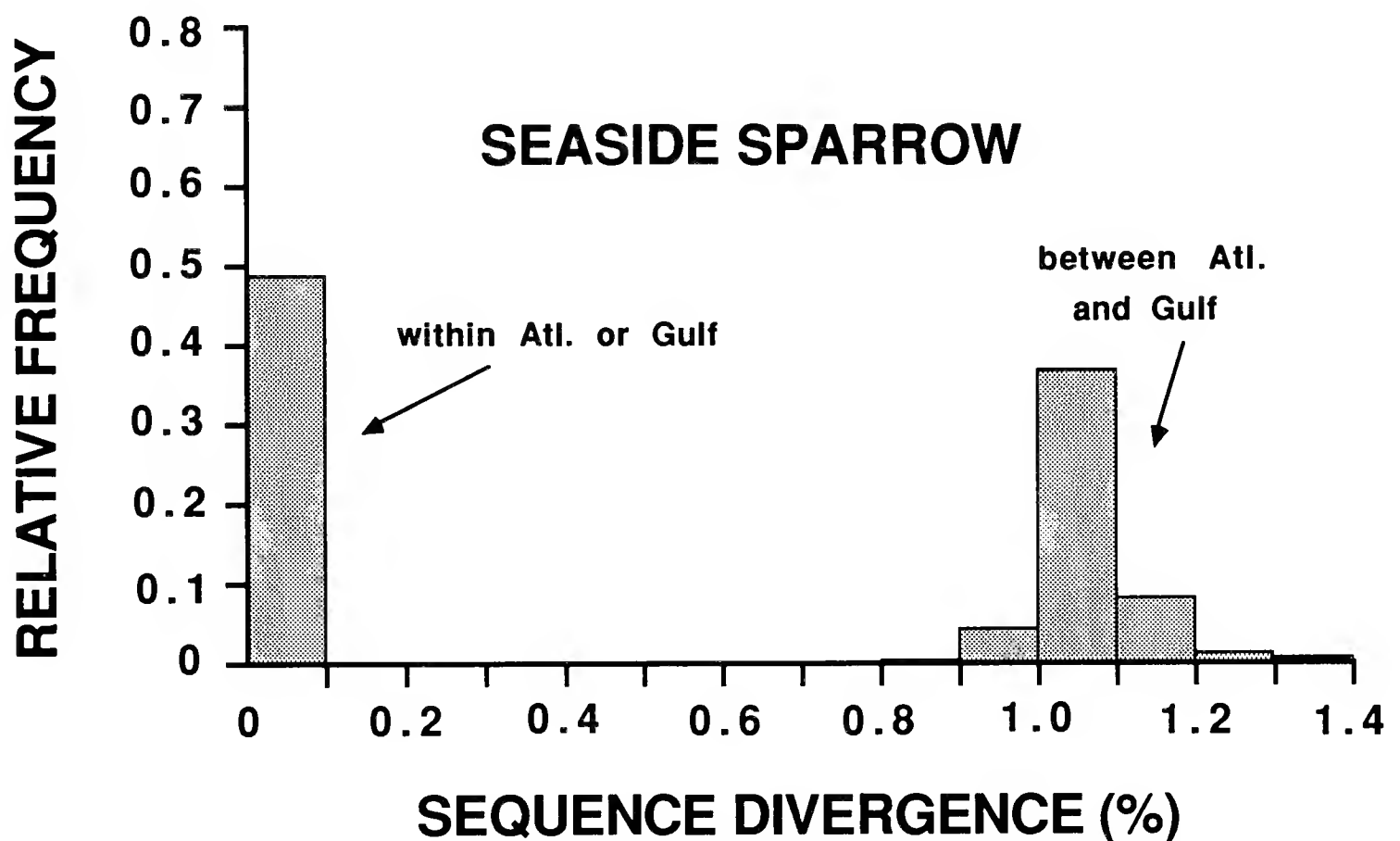


FIGURE 2 - Frequency distribution of mtDNA genetic distances observed in 780 pairwise comparisons among 40 Seaside Sparrows collected from localities along the Atlantic and Gulf coasts.

Phylogeographic category II

A phylogeographic pattern until recently not reported in any animal species is that in which highly distinct mtDNA clones or clades co-occur as polymorphisms over a broad geographic area. We recently have found two such examples, involving the Snow Goose *Anser caerulescens* (Avisé & Alisauskis in prep) and the Mallard Duck *Anas platyrhynchos* (Avisé et al. 1990). In the Snow Goose, a survey of major breeding locales across the species' range in Arctic Canada revealed two distinct mtDNA clades ($p \approx 0.011$) shared by all surveyed populations (albeit in significantly different frequencies). Similarly, populations of Mallard from California and Manitoba shared distinct mtDNA clades differing by $p \approx 0.009$.

The origins of such mtDNA differences are unclear, although they may indicate effects of past population disjunction and recent admixture. The results are somewhat surprising, because most gene flow in waterfowl (Anatidae) is thought to be mediated by males, who pair with females on wintering grounds or during migration, and move to the female's natal colony to breed (Cooke et al. 1975). Nevertheless, the mtDNA results suggest recent connectedness among colonies involving females. The finding that mtDNA lines are shared between locales in some waterfowl, where dispersal is presumably male-biased, makes even more impressive the sharp mtDNA phylogeographic discontinuities observed in other avian species (such as the Seaside and Sharp-tailed Sparrows).

CONCLUSIONS ABOUT AVIAN POPULATION STRUCTURE

The mtDNA phylogeny of any species represents but one realization of the process of gene lineage sorting through an organismal pedigree, and hence must be interpreted with caution as an indicator of overall genomic (nuclear) history. In the absence of concordant support from independent evidence, significant partitions in an mtDNA phylogeny cannot necessarily be assumed to evidence fundamental historical subdivisions at the population level (Avice and Ball 1990). One form of support can come from a correspondence between mtDNA phylogenetic subdivisions and boundaries between historical biogeographic provinces (a good example involves the Seaside Sparrow). Or the support may derive from concordance of subdivisions in the mtDNA gene tree with those registered in other attributes such as morphology (a good example involves the large- and small-bodied forms of the Canada Goose – Van Wagner and Baker 1990). In other cases, confidence must rest on plausibility arguments – for example, given the current widespread distribution of the Red-winged Blackbird, its potential for long-distance movement, and the fact that major portions of its range were uninhabitable only 13,000 years ago, the species may indeed have expanded its range and population size in recent evolutionary times, as the mtDNA data strongly suggest.

In interpreting gene phylogenies, a distinction should also be drawn between generalized conclusions about the magnitude of population structure, versus the evidence for particular historical population separations. In species whose populations exhibit contemporary isolation by distance in the absence of long-standing biogeographic barriers to dispersal, phylogenies of independent genes may each reveal significant population subdivision, yet exhibit little concordance in the population units identified. Such results imply generalized restrictions on gene flow, but the particular populations recognized by any gene may be of little evolutionary consequence. However, when populations or regions are concordantly identified by independent genes, long-standing biogeographic separations are strongly implicated (Avice & Ball 1990).

With these caveats in mind concerning inferences from mtDNA (or other) gene trees, the following conclusions about avian population structure can be drawn from the mtDNA data currently available:

- 1) Most avian species exhibit a wealth of intraspecific polymorphism, although still far less than predicted under neutrality theory given current population sizes and presumed rate of mtDNA evolution. Thus either: (a) directional selection favoring particular genotypes has served periodically to reduce the level of mtDNA

polymorphism; or (b) evolutionary effective population sizes are comparatively low for other reasons involving historical demography (such as fluctuations in numbers of successfully-breeding females).

- 2) Populations of some avian species, such as the Red-winged Blackbird, are characterized by considerable historical connectedness over recent evolutionary time, as judged by limited mtDNA phylogeographic structure. Within some such species, extensive morphological differentiation appears to have arisen against a relatively shallow phylogenetic backdrop.
- 3) Other avian species, such as the Seaside Sparrow, consist of regional populations exhibiting strong phylogenetic separation. Inter-regional genetic distances are much larger than those observed within regions, and the phylogenetic gaps tend to correlate with likely biogeographic partitions. Thus historical population separation (rather than retention of ancient lineages within a large, non-subdivided population) probably accounts for such major mtDNA phylogeographic discontinuities.
- 4) In some species (such as the Snow Goose, and perhaps the Mallard Duck), distinct mtDNA lineages are shared by widely separated breeding populations. Waterfowl are unusual among birds in the strength of female site philopatry and degree of male-biased dispersal between breeding areas. Since extant populations of such species can exhibit relatively high levels of connection in a matriarchal genealogy, estimates of contemporary female movement (e.g., through results of direct observations or banding returns) may sometimes be quite misleading as indicators of the magnitude of historical interpopulation gene flow.
- 5) Avian populations appear to be structured at a variety of evolutionary timescales. In addition to the deep mtDNA phylogeographic structures of some species, which probably evidence long-term biogeographic separations, many populations also show significant haplotype frequency differences, suggesting further restrictions on gene flow over ecological timescales. Such contemporary structure is consistent with the limited realized vagility of most bird species relative to the size of their respective ranges, and probably represents a general isolation by distance rather than long-term vicariant separations of singular significance.

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POPULATION DIFFERENTIATION IN NEW ZEALAND BIRDS

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ABSTRACT. Because New Zealand is an archipelago of three main islands with numerous offshore islands, many species of birds are fragmented into disjunct populations. The destruction of habitats and the introduction of mammalian predators by humans in the last 1000 years has further fragmented populations and reduced population sizes. Avian species that were once widely distributed, or still are, on the main islands often show clinal (Little Blue Penguin) or regional (Brown Kiwi, Yellow-crowned Parakeet) genetic differentiation. Main island species with naturally limited dispersal (Blue Duck) show local differentiation, as do some island isolates (Red-crowned Parakeet, Brown Teal, Yellow-eyed Penguin). Environmental alteration appears to contribute significantly to inter-specific hybridisation threatening some native species (Black Stilt, Forbes Parakeet, Grey Duck). Geographic patterns of genetic variation do not support present taxonomic classifications of some species.

Keywords: New Zealand birds, allozymes, systematics, geographic variation, population differentiation, hybridisation.

INTRODUCTION

New Zealand has been isolated from all other landmasses since its separation from Gondwanaland about 80 million years ago (Stevens et al. 1988). This has led to a distinctive avifauna of approximately 300 species (Robertson 1985), including one endemic order, five endemic families, and 24 endemic genera. About 50 more species, including many endemics and such spectacular species as the moas (*Dinornithiformes*) and the Giant Eagle (*Harpagornis*), have become extinct since the arrival of humans about 1000 years ago.

Ancient endemics such as Kiwi¹ *Apteryx*, Kakapo *Strigops habroptilus*, New Zealand Wrens (*Xenicidae*), and Wattlebirds (*Callaeidae*) are not closely related genetically to other birds and have evolved unique morphological and behavioural features. On the other hand, much of the avifauna arrived in New Zealand in more recent evolutionary times (e.g., Parakeets, *Cyanoramphus* spp.; Stilts, *Himantopus* spp.), and these species clearly show their affinities to overseas relatives. Since about 1850 some Australian species have established, apparently without human assistance (e.g., Welcome Swallow, *Hirundo tahitica*; Silvereye, *Zosterops lateralis*), and other species have been human-assisted settlers (e.g., House Sparrow, *Passer domesticus*; Starling, *Sturnus vulgaris*; Indian Myna, *Acridotheres tristis*).

In this paper we summarise and discuss patterns and levels of intra-specific differentiation of the extant New Zealand avifauna, focusing on native species for which

¹ Common and scientific names follow Kinsky (1970) or Robertson (1985), unless otherwise stated.

genetic (usually allozyme) data are available. We relate these patterns to the recent ecological history of New Zealand and inferred historical patterns of distribution. Allan Baker and co-workers have assessed in detail the population differentiation of assisted immigrants (e.g., House Sparrow, Baker 1980; Indian Myna, Baker and Mooed 1979, 1987; Starling, Ross 1983); we do not deal with these species here.

SYSTEMATICS AND POPULATION DIFFERENTIATION

Taxonomies describe the distribution of variation in natural populations, both within and between species (Corbin 1983). In recent decades the primary sources for taxonomy of New Zealand birds have been Oliver (1930, 1955) and Kinsky (1970). These landmark volumes and the sources they draw upon often suffer from the general problems described by Avise (1989) in identifying species and subspecies on the basis of few morphological traits, often not explicitly specified, and using outdated or unstated species or subspecies concepts.

Taxonomy is the essential foundation for conservation practice, and instances of incorrect taxonomies have had costly consequences for conservation (Avise 1989, Avise & Nelson 1988, Daugherty et al. 1990a). Systematic analyses of New Zealand reptiles (Daugherty et al. 1990a, 1990b, Patterson & Daugherty 1990, R.A. Hitchmough, pers. comm.) using both allozyme and morphological characters have led to discovery of numerous cryptic species and re-assessment of the conservation status of many taxa. Taxonomic classifications of many New Zealand bird taxa have not been subjected to analysis using genetic data and contemporary systematic methodologies and may thus require significant revision.

Genetic data have already revealed inadequacies in some longstanding taxonomic assessments of New Zealand birds. For example, Meredith and Sin (1988) demonstrated clinal variation in both allozyme and morphological characters of Blue Penguins *Eudyptula minor* along the east coast of both main islands, a pattern conflicting with the present division of Blue Penguins into five subspecies (Robertson 1985).

Similarly, genetic data do not support the present taxonomy of Brown Kiwi. As many as eight species of kiwis were described last century. Oliver (1930) accepted four species, including two species of Brown Kiwi: *Apteryx mantelli*, the North Island Brown Kiwi, and *A. australis*, the South and Stewart Island Brown Kiwi. However, Oliver (1955) merged all Brown Kiwis into a single species, *A. australis*, with three subspecies (North Island, South Island, Stewart Island). The pattern of allozyme variation (C.H. Daugherty et al., unpubl. data) agrees with the former taxonomy in defining two main geographic groups; a "North Island" type occurs as far south as Okarito on the west coast of the central South Island, and a second type occurs in Fiordland and Stewart Island.

Parakeets provide a third instructive case. Allozyme variation in *Cyanoramphus* parakeets demonstrated that the endangered Chatham Island Yellow-crowned (or Forbes') Parakeet is not a subspecies of the Yellow-crowned Parakeet *C. auriceps* as classified by Oliver (1930, 1955), but is instead a full species *C. forbesi* as originally described (Triggs & Daugherty, in press). Forbes' Parakeet is most closely related to the Red-crowned Parakeet *C. novaezelandiae novaezelandiae*, with which it co-occurs.

A complete study of differentiation in either Red-crowned or Yellow-crowned Parakeets could thus not be undertaken without first knowing the relationships of Forbes' Parakeet.

These examples demonstrate the necessity for basing conservation practice on accurate taxonomies. Surveys of population differentiation, even in taxa of the highest conservation significance, may often produce surprising results (Daugherty et al. 1990a). We expect that the use of formal systematic methodologies and new types of data, especially genetic data, will identify further inadequacies in the taxonomy of New Zealand birds.

GEOGRAPHIC DISTRIBUTION AND POPULATION DIFFERENTIATION

Until the arrival of humans, forest habitats were continuous over much of mainland New Zealand (Stevens et al. 1988). Human activity has reduced the forest cover of the two main islands from perhaps 85% to less than 25%. Farmlands and exotic forest plantations have replaced indigenous forests. Lowland forest habitats are mostly small, isolated fragments. These changes have made the landscape more suitable for many introduced species and less satisfactory for natives. Many introduced mammalian species are efficient predators on native birds, especially the flightless ones. Introduced birds are probably often effective competitors of native species.

All these factors have altered distributions of native bird species. In this section we relate present patterns of geographic distribution to data on population differentiation. Species are arbitrarily categorised into five groups, on the basis of increasingly fragmented levels of historical geographic distribution. Thus, the extent of differentiation of conspecific populations could be expected to increase with each group.

Geographically widespread, relatively abundant species

Despite fragmentation of habitats, some native species such as Pukeko *Porphyrio porphyrio*, Tui *Prothemadera novaeseelandiae*, and Bellbird *Anthornis melanura* still occur widely throughout one or both islands. These species have adapted to modified habitats and, in the case of the Pukeko that occupies farmland, may be far more widely distributed than in pre-human times.

Two species in this category are the Blue Penguin and Brown Kiwi, both discussed earlier. The Blue Penguin appears to be highly variable over its entire range, but breeding populations diverge in a gradual, clinal fashion (Meredith & Sin 1988), as might be expected for abundant, geographically continuous populations.

Brown Kiwi probably occurred continuously throughout all three main islands until the arrival of Europeans. Still limited to forests, they occur widely only where forests are extensive as in Fiordland and Stewart Island. In the North Island, Brown Kiwis are sometimes abundant in exotic pine plantations. Preliminary allozyme studies of small numbers of individuals from widely scattered locations throughout the entire range of Brown Kiwis (Daugherty et al., unpubl. data) reveal the two major geographic groups noted earlier. Taxonomic status of the two groups remains to be determined, but the level of differentiation (Nei's $D = 0.05$) is about that often associated with speciation in birds (Barrowclough & Corbin 1978, Avise et al. 1980, Barrowclough 1983).

Sample sizes are too small to resolve patterns of local variation. Nonetheless, polymorphisms are sufficiently common to suggest that genetic structuring may occur within the two main groups of Brown Kiwi.

Geographically widespread species; populations once continuous, but now fragmented due to recent reductions in numbers or habitats

Species in this category include mainland populations of Red-crowned Parakeets, Yellow-crowned Parakeets, and Weka *Gallirallus australis*. Genetic studies of Weka may be particularly revealing, as this species is presently separated into four subspecies that show significant colour variation (Robertson 1985). There may be some urgency to study Weka, as numbers appear to be diminishing throughout its present range.

Genetic data for Yellow-crowned Parakeets (Triggs & Daugherty, in press) show that the species is apparently divided into two main geographic groups, one from the North Island and northern South Island, and a second from the central and southern South Island, a pattern generally resembling that of Brown Kiwis. The level of differentiation ($D = 0.02$) is roughly that associated with subspecies and sometimes species of birds.

Variation in Yellow-crowned Parakeets must also take into account the extremely rare Orange-fronted Parakeet, originally described as a separate species *C. malherbi* but considered by many recent workers to be a colour morph of the Yellow-crowned Parakeet (Holyoak 1974, Taylor et al. 1986). Differences in allozyme frequencies exist between sympatric populations of Orange-fronted and Yellow-crowned Parakeets, but sample sizes are too small to allow statistical testing (Triggs & Daugherty in press). In view of the relatively limited genetic differentiation commonly found between congeneric species of birds (e.g., Barrowclough & Corbin 1978; Avise et al. 1980), reduction of the taxonomic status of Orange-fronted Parakeets is premature.

Formerly widespread species; numbers now greatly reduced

Many species restricted to diminishing habitats such as forests are now greatly reduced in numbers and distribution, e.g., Kokako *Callaeas cinerea*, Little Spotted Kiwi *Apteryx owenii*, Kakapo, Blue Duck *Hymenolaimus malacorhynchos*, Saddleback *Philesturnus carunculatus*, and Stitchbird *Notiomystis cincta*. All were widespread until European times; some (Little Spotted Kiwi, Saddleback, Stitchbird) now survive only on a few offshore islands.

The Little Spotted Kiwi, once found widely on both main islands, now survives in one population of some hundreds on Kapiti Island, and in several much smaller island populations originating from translocations of Kapiti Island birds. Comparison of allozymes of a single wild individual discovered on D'Urville Island with birds from Kapiti Island showed no difference (C.H. Daugherty & R. Colbourne, unpubl. data).

Fewer than 50 Kakapo now survive. Comparison of allozyme frequencies of a population in Fiordland, where numbers have been reduced to just a few individuals, with a population from Stewart Island numbering about fifty birds, showed no significant differences (Triggs et al. 1989). Average heterozygosity in the Stewart Island population ($H = 0.04$) was similar to the average for other avian species (Barrowclough 1983, Barrowclough et al. 1985), while that of the Fiordland population was somewhat lower ($H = 0.02$), possible evidence of the genetic bottleneck.

Blue Duck populations have been studied by both allozyme and DNA methodologies (Triggs et al. in press). This species was widespread in pre-European times, and its riverine distribution was essentially one-dimensional. DNA fingerprinting studies indicate that local populations consist of highly interrelated individuals, a result of strong natal philopatry and perhaps also recent isolation into river headwaters. Thus, extensive genetic differentiation occurs over relatively short distances in this species.

Geographically widespread, naturally fragmented populations

This type of distribution characterises species that occur on the outlying islands of New Zealand, especially the sub-Antarctic islands. They might be expected to show higher levels of population differentiation than species with continuous or recently fragmented distributional patterns. Very different levels of divergence characterise the two taxa examined genetically thus far.

Red-crowned parakeets occur on most major outlying island groups, and variation in blood allozymes has been investigated in detail (Triggs & Daugherty in press). Genetic differentiation between island groups is low ($D < 0.02$), in line with levels found between subspecies and conspecific populations of other birds (Barrowclough 1983). The single individuals sampled of the Kermadec Parakeet *C. n. cyanurus* and Reischek's parakeet *C. n. hochstetteri* from the Antipodes Islands, over 2000 km distant from one another, are identical at 21 loci examined. Populations of the New Zealand Red-crowned Parakeet *C. n. novaezelandiae* on three island groups near the North Island (Three Kings Islands, Poor Knights Islands, Little Barrier Island) are highly polymorphic at five of these loci but little differentiated, clustering as each other's closest relatives in support of their present taxonomic classification. The low levels of genetic differentiation may reflect recent occupation of islands by this species, or it may indicate recurrent gene flow and large population sizes.

Allozyme variation in one of the world's rarest penguins, the Yellow-eyed Penguin (*Megadyptes antipodes*; fewer than 3000 breeding individuals), have been compared from three widely separated locations (the east coast of the South Island, Campbell Island, and Enderby Island in the Auckland Island group). Differentiation among these groups ($F_{ST} = 0.24$, Triggs & Darby 1989) was about an order of magnitude higher than among other geographically widespread species of birds (Barrowclough 1983), indicating that gene flow among the three locations is extremely limited. In marked contrast to the relatively undifferentiated Red-crowned Parakeets, however, the high levels of genetic differentiation in Yellow-eyed Penguins are not reflected in any taxonomic subdivision into subspecies.

Species with naturally limited distributions

Many island endemic populations of species, such as the rare Chatham Island Black Robin *Petroica traversi*, may always have been small. Studies of these island isolates may reveal little differentiation from their closest relatives, as found, for example, among some island populations of the Red-crowned Parakeets. The Forbes' Parakeet shows limited differentiation ($D = 0.01$) from its probable closest relative, the sympatric Chatham Island Red-crowned Parakeet (Triggs & Daugherty in press). This suggests a recent origin for the taxon, although the situation is confounded by recent interbreeding between the species.

Levels of differentiation can also be high. Brown Teal *Anas aucklandica*, for example, are presently separated into three subspecies (mainland New Zealand, Auckland Is-

lands, and Dent Island in the Campbell Island group). Allozyme divergence among these subspecies ($D = 0.07-0.15$) substantially exceeds the level usually associated with subspecies, suggesting that these taxa deserve full specific recognition (M.J. Williams et al., unpubl. data).

HYBRIDISATION

In addition to geographic distribution, hybridisation also affects differentiation within genera or species of some New Zealand birds. Three cases of hybridisation, all originally recognised by the presence of morphologically intermediate birds, have now been investigated using allozymes. All are associated with human modification of natural habitats and are of conservation significance.

Grey Duck

In recent decades, numbers of the introduced Mallard, *Anas platyrhynchos*, have increased throughout New Zealand at the expense of the native Grey Duck, *Anas superciliosa*. Mallards now outnumber Grey Duck by 4:1 throughout the country (Robertson, 1985). Allozyme analysis (Hitchmough et al. 1990) showed virtually no polymorphism and thus no detectable genetic difference between birds characterised morphologically as Grey Ducks, Mallards, or hybrids. The absence of polymorphism in Mallards is surprising in view of relatively high heterozygosity ($H = 0.05$) in North American populations (Ankney et al. 1986). Grey Ducks may persist because hybrids mate preferentially with Mallards. On the other hand, the numerical imbalance favouring Mallards may eventually lead to the demise of Grey Ducks.

Black Stilts

The Black Stilt, *Himantopus novaezelandiae*, has experienced a severe decline following introduction of numerous mammalian predators, to which it seems especially susceptible, and extensive habitat changes associated with European settlement. The latter may have favoured the Pied Stilt, *Himantopus h. leucocephalus* which has greatly expanded its range and numbers (Robertson 1985). The two species have hybridised extensively (Pierce 1984).

Allozyme studies showed that the few (~50) remaining Black Stilts are genetically distinct from Pied Stilts despite the extensive history of hybridisation (Green 1988); that is, Blacks are not simply a colour morph of Pied Stilts. Captive breeding programmes to save the Black Stilt are now a central focus of its management.

Parakeets

The best known instance of hybridisation among New Zealand birds involves Forbes' and Red-crowned Parakeets on Mangere and Little Mangere Islands in the Chatham Islands group. Habitat changes that reduced optimum habitat for Forbes' Parakeets may be the cause of hybridisation that threatened the Forbes' Parakeet, which occurred only on these two small islands (Cade 1983). The New Zealand Wildlife Service responded with a programme to remove (by shooting) all Red-crowned Parakeets and hybrids from these islands, and to re-establish suitable habitat for the Forbes'.

Allozyme studies (Triggs & Daugherty in press) showed that morphologically "pure" Forbes' Parakeets have retained their genetic distinctness from Red-crowned Parakeets, probably because hybrids breed mainly with Red-crowned Parakeets.

Barriers to hybridisation may be low among New Zealand *Cyanoramphus* Parakeets. Hybrids of Red-crowned and Yellow-crowned Parakeets have now been identified on Little Barrier Island (Triggs & Daugherty in press), and most birds on the Auckland Islands have recently been reported to be hybrids of these two species (Taylor 1985, G. Elliott, pers. comm.). The demise of the Orange-fronted Parakeet, if it is truly a distinct species, could also be the result of hybridisation with the Yellow-crowned Parakeet (Triggs & Daugherty in press).

CONCLUSIONS

Few studies of geographic variation and population differentiation in New Zealand birds have used either contemporary systematic methodologies or genetic data. Existing taxonomies often do not adequately describe variation for taxa where such studies have been conducted, e.g., Brown Kiwi, Blue Penguins, Yellow-crowned Parakeets, Yellow-eyed Penguins, and Brown Teal. Systematic studies of geographic variation can be expected to contribute much to conservation of species yet to be examined similarly, such as Weka and Great Spotted Kiwi *Apteryx haastii*.

Human habitation of New Zealand has greatly reduced forest habitats for birds. At the same time, new habitats (farmlands, pine plantations) have been occupied either by self-introduced species from Australia or by human-introduced species that may compete with native species. Populations of native birds have been reduced and their distributions fragmented.

Nonetheless, patterns of differentiation of native birds can often be related to probable pre-human patterns of distribution. Prior to human occupation of New Zealand, species such as the Brown Kiwi and Yellow-crowned Parakeet, for example, occurred continuously over wide areas. Present limited differentiation among populations of the North Island and northern South Island supports an inference of high recent levels of gene flow. Similarly, the Blue Penguin, distributed more or less continuously down the east coast of both main islands, shows clinal differentiation in morphology and allozymes.

Some geographic barriers seem to have had limited effect in isolating populations. Cook Strait, for example, appears to have been no barrier to gene flow in either Yellow-crowned Parakeets or the flightless Brown Kiwi, a pattern also found in the widely distributed New Zealand common skink, *Leiopisma nigriplantare* (Daugherty et al. 1990b). Lack of significant population differentiation in Red-crowned Parakeets between some oceanic islands may reflect either recency of invasion of these locations or recent gene flow and large population sizes.

On the other hand, social structure (Blue Duck) and geographic barriers (Yellow-eyed Penguins, Brown Teal) may function to limit gene flow and lead to infra-specific differentiation of some avian species.

Finally, recent habitat alterations are associated with hybridisation, primarily among taxa that were poorly differentiated to begin with. For Forbes' Parakeets, Black Stilts, and Grey Ducks, the weakness of barriers to hybridisation places their future in doubt.

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PHENETIC VARIATION IN NEARCTIC EMBERIZINAE

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ABSTRACT. I examined phenetic relationships, based on 24 skeletal measures, of 42 taxa (of 36 currently recognized species) in 15 genera of North American Emberizinae. In spite of the taxonomic diversity of the group, they seem to be remarkably similar in proportions, differing among taxa primarily in size. Nonetheless, taxa that live in short-grass or short tundra habitats, in which high winds are characteristic, seem to have relatively long wings, short toe bones (though long claws), and relatively short, conical bills. Marsh-dwelling species, on the other hand, tend to have relatively short wings, long legs and toes, and long bills. In general, species within a genus cluster together, although there is commonly a great deal of overlap among genera. The variability among populations of the Savannah Sparrow is as great as that among species in other genera. Closely related species that co-occur in the same habitat often are quite similar in size and proportions, indicating that interspecific competition has not played an important role in the evolution of morphological differences among species in this group.

Keywords: Emberizinae, phenetic similarity, habitat overlap.

INTRODUCTION

The Emberizinae (Emberizidae), or Old World Buntings and New World Sparrows, contain 65 recognized genera and 279 species, and thus are one of the largest sub-families of birds (containing about 3% of all avian species) (Bock & Farrand 1980). The group is well represented in the Nearctic: 17 genera and 47 species breed and occur regularly north of Mexico (AOU Check-list of North American Birds, 1983).

Here I examine phenetic variation among a wide range of taxa of North American sparrows, buntings, and longspurs, and relate this variability to the interspecific and, in two instances, the intraspecific variation in typical habitat use and behaviour of the populations.

METHODS

The species and populations measured for the phenetic analyses are listed in Table 1. Most of the specimens measured were collected recently and prepared as skin-and-skeleton specimens, and donated to the Royal Ontario Museum, but additional material was borrowed from several other museums (see list in Acknowledgements) to augment samples so that at least 10 individuals were measured for all but one of the taxa. For this paper, only data on males are reported; all of these species are sexually dimorphic in size (Rising in prep.), and numbers of specimens of females available are generally substantially smaller than numbers of male specimens.

I measured the 24 features listed in Table 2 on the prepared skeleton of each specimen. Measurements were taken to the nearest 0.1 mm, and were taken as illustrated by Robins & Schnell (1971), with the following exceptions: premaxilla length is from

the anterior edge of the narial opening; premaxilla depth is maximal depth of the premaxilla; and synsacrum width is the distance between the antitrochanters. In general, interpopulational variation in size is not considered in this study. Nonetheless, because of considerable geographic variation in size in many of these species, care was taken to use only specimens from a limited region for conspicuously variable species (Table 1). Several populations of some notably polytypic species were used when sufficient material was available. Specifically, four populations of Savannah Sparrows (*Passerculus sandwichensis* s. l.) and Sharp-tailed Sparrows (*Ammodramus caudacutus* s. l.) were used. In both instances these represent well differentiated taxa that have, at various times, been recognized as different species or at least as well-marked subspecies. These were the "Ipswich" Sparrow (*P. s. princeps*), "typical" Savannah Sparrow (*P. s. labradorius*), "Belding's" Sparrow (*P. s. beldingi*), and "Large-billed" Sparrow (*P. s. rostratus*); and "typical" Sharp-tailed Sparrow (*A. c. caudacutus*), "James Bay" Sharp-tailed Sparrow (*A. c. altera*), "Nelson's" Sparrow (*A. c. nelsoni*), and "Acadian" Sharp-tailed Sparrow (*A. c. subvirgata*).

TABLE 1 – Species, numbers, and samples of Emberizine sparrows, buntings, and longspurs measured for phenetic analyses

Species	N	Localities from which specimens taken
Green-tailed Towhee <i>Pipilo chlourus</i>	8	Az(5); Tx(2); Id(1)
Rufous-sided Towhee <i>P. erythrophthalmus</i>	11	Ks(4); De(3); Ont(3); Ma(1); Mo(1)
Bachman's Sparrow <i>Aimophila aestigalis</i>	10	Tx(4); Fl(4); Ky(2)
Cassin's Sparrow <i>A. cassini</i>	17	Tx(9); NM(5); Ks(3)
Rufous-winged Sparrow <i>A. carpalis</i>	19	Mex(11); Az(8)
Rufous-crowned Sparrow <i>A. ruficeps</i>	10	Tx(5); Mex(3); NM(1); Az(1)
American Tree Sparrow <i>Spizella arborea</i>	10	Man(5); Ont(4); Ak(1)
Chipping Sparrow <i>S. passerina</i>	11	Ont(10); Mo(1)
Clay-colored Sparrow <i>S. pallida</i>	15	Sask(15)
Brewer's Sparrow <i>S. breweri</i>	11	Az(3); Tx(1); Alta(1); Co(1); Ok(1); Mt(1); Mex(1)
Field Sparrow <i>S. pusilla</i>	11	Ks(5); Ont(4); Ar(1); Tx(1)
Vesper Sparrow <i>Pooecetes gramineus</i>	35	Sask(11); Tx(6); Alta(4); Az(3); ND(3); Ont(3); WVa(2); BC(1); Ca(1); Nv(1)
Lark Sparrow <i>Chondestes grammacus</i>	14	Tx(6); Ks(4); Wy(2); Ca(1); NM(1)
Black-throated Sparrow <i>Amphispiza bilineata</i>	10	Az(5); Tx(3); NM(2)
Lark Bunting <i>Calamospiza melanocorys</i>	32	Tx(16); Sask(9); Ks(5); Ok(2)
Savannah Sparrow <i>Passerculus sandwichensis labradorius</i>	49	Moosonee, Ontario

TABLE 1 – continued

Species	N	Localities from which specimens taken
"Ipswich" Sparrow <i>P. s. princeps</i>	17	Sable Is., Nova Scotia
"Belding's" Sparrow <i>P. s. beldingi</i>	21	Bahia de San Quintin, Baja Cal. N.
"Large-billed" Sparrow <i>P. s. rostratus</i>	20	Bahia Kino, Sonora
Baird's Sparrow <i>Ammodramus bairdii</i>	29	Sask(14); ND(12);
Grasshopper Sparrow <i>A. savannarum</i>	21	ND(8); Tx(4); WVa(4); Az(2); Ks(1); NB(1); Ont(1)
Henslow's Sparrow <i>A. henslowii</i>	15	Mi(5); Ks(4); Md(2); Oh(2); Ont(2)
LeConte's Sparrow <i>A. leconteii</i>	31	ND(10); Ont(10); Ks(8); Ky(1); Man(1)
Sharp-tailed Sparrow <i>A. c. caudacutus</i>	21	Prime Hook Refuge, Delaware
"Acadian" Sharp-tailed Sparrow <i>A. c. subvirgata</i>	17	Sackville, New Brunswick
"James Bay" Sharp-tailed Sparrow <i>A. c. altera</i>	20	Moosonee, Ontario
"Nelson's" Sharp-tailed Sparrow <i>A. c. nelsoni</i>	14	Upham, North Dakota
Seaside Sparrow <i>A. maritimus</i>	31	De(17); NC(7); NJ(6); NY(1)
Fox Sparrow <i>Passerella iliaca</i>	19	Ont(9); Ks(6);
Song Sparrow <i>Melospiza melodia</i>	16	Ont(6); NB(3); Que(3); Man(2); Ok(1); WVa (1)
Lincoln's Sparrow <i>M. lincolnii</i>	13	Ont(10); Que(2); Nfld(1)
Swamp Sparrow <i>M. georgiana</i>	12	Ont(7); Mi(4); Nfld(1)
White-throated Sparrow <i>Zortotrichia albicollis</i>	10	Ont(10)
Golden-crowned Sparrow <i>Z. atricapilla</i>	11	BC(7); Ca(4)
White-crowned Sparrow <i>Z. leucophrys</i>	72	NWT(29); Que(25); Man(18)
Harris's Sparrow <i>Z. querula</i>	12	Ks(8); NWT(4)
Dark-eyed Junco <i>Junco hyemalis</i>	33	Ont(33)
McCown's Longspur <i>Calcarius mccownii</i>	18	Sask(8); Mt(5); Alta(3); Ks(2)
Lapland Longspur <i>C. lapponicus</i>	19	Coppermine, NWT
Smith's Longspur <i>C. pictus</i>	14	Ont(7); NWT(4); Man(3)
Chestnut-collared Longspur <i>C. ornatus</i>	21	Alta(6); Sask(6); ND(4); Mt(2); Tx(2); Ks(1)
Snow Bunting <i>Plectrophenax nivalis</i>	10	Mi(6); Ont(3); Ak(1)

TABLE 2 – Correlations between 24 variables and principal component 1 and principal component 2 scores for four Emberizid samples (correlations < 0.35 are not Printed)

Variable	Principal Component 1				Principal Component 2			
	All	A ^a	B ^b	C ^c	All	A	B	C
Skull Length	.91	.68	.95	.97	-.36	-.72		
Skull Width	.91	.95	.96	.95				
Premaxilla Length	.68	.56	.90	.83	-.54	-.83		.42
Premaxilla Depth	.86		.94	.93				
Narial Width	.93	.75	.98	.96		.49		
Premaxilla Width	.87		.95	.85		.59		.52
Interorbital Width	.77	.45	.85	.89		-.55		
Mandible Length	.89	.62	.94	.95	-.39	-.77		
Gonys Length	.61	.52	.90	.66	-.68	-.79		.67
Mandible Depth	.86	.41	.93	.85				
Coracoid Length	.96	.94	.93	.85				
Scapula Length	.92	.88	.97	.89	.36	.45		-.42
Femur Length	.91	.84	.94	.95		-.47		
Femur Width	.91	.93	.93	.95				
Tibiotarsus Length	.89	.76	.92	.91		-.51		
Tarsometatarsus Length	.86	.82	.89	.88		-.35		
Humerus Length	.95	.95	.98	.83				.39
Ulna Length	.80	.76	.85	.83	.55	.62	.49	
Carpometacarpus Length	.82	.76	.90	.61	.54	.52	.40	-.73
Hallux Length	.48	.75	.82		-.49		-.50	
Sternum Length	.93	.84	.96	.98	.35	.52		
Sternum Depth	.77	.65	.84	.88	.56	.71	.51	
Keel Length	.87	.74	.92	.96	.45	.64	.36	
Synsacrum Width	.93	.87	.98	.68				-.68
% Variance Explained	72.6	54.4	85.5	75.0	13.2	26.0	7.7	11.4

^a*Passerculus* & *Ammodramus*; ^b*Aimophila*, *Spizella*, *Chondestes*, *Amphispiza*, *Passerella*, *Melospiza*, *Zonotrichia*, & *Junco*; ^c*Poocetes*, *Calamospiza*, *Calcarius*, & *Plectrophenax*

Averages were calculated for each measured character and each taxon, and these averages were used in phenetic analyses. Thus, variability within the samples is not assessed here. I used Principal Components Analysis (PCA) (NT-SYS Factor; Rohlf 1985), operating on a matrix of correlations among non-standardized or transformed measurements to extract multivariate measures of size and shape variation among species. This is one of several more-or-less equally suitable methods that could be used for our objectives (Rising & Somers 1989).

In addition to summarizing variation among all 42 samples (of 36 species recognized by the 1983 AOU Check-list), I subdivided the samples into three smaller sets in order to focus attention on the variability within those groups. These groups were:

- (A) The *Passerculus* and *Ammodramus* group, several presumably closely-related species that live in grassland or in sedge or grass marshes.
- (B) The *Aimophila*, *Chondestes*, *Amphispiza*, *Spizella*, *Passerella*, *Melospiza*, *Zonotrichia* and *Junco* group, 20 species that occur in a variety of different

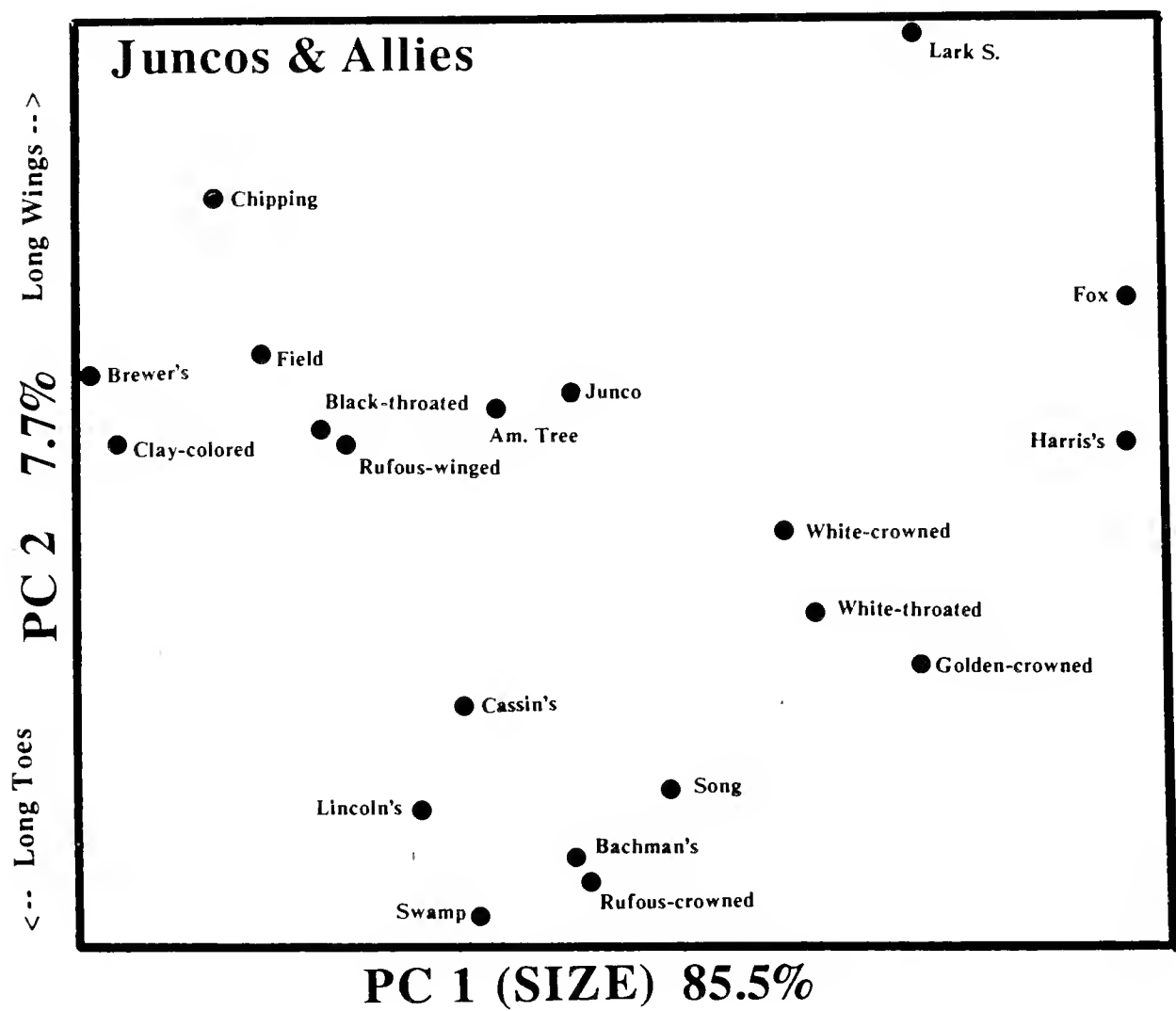
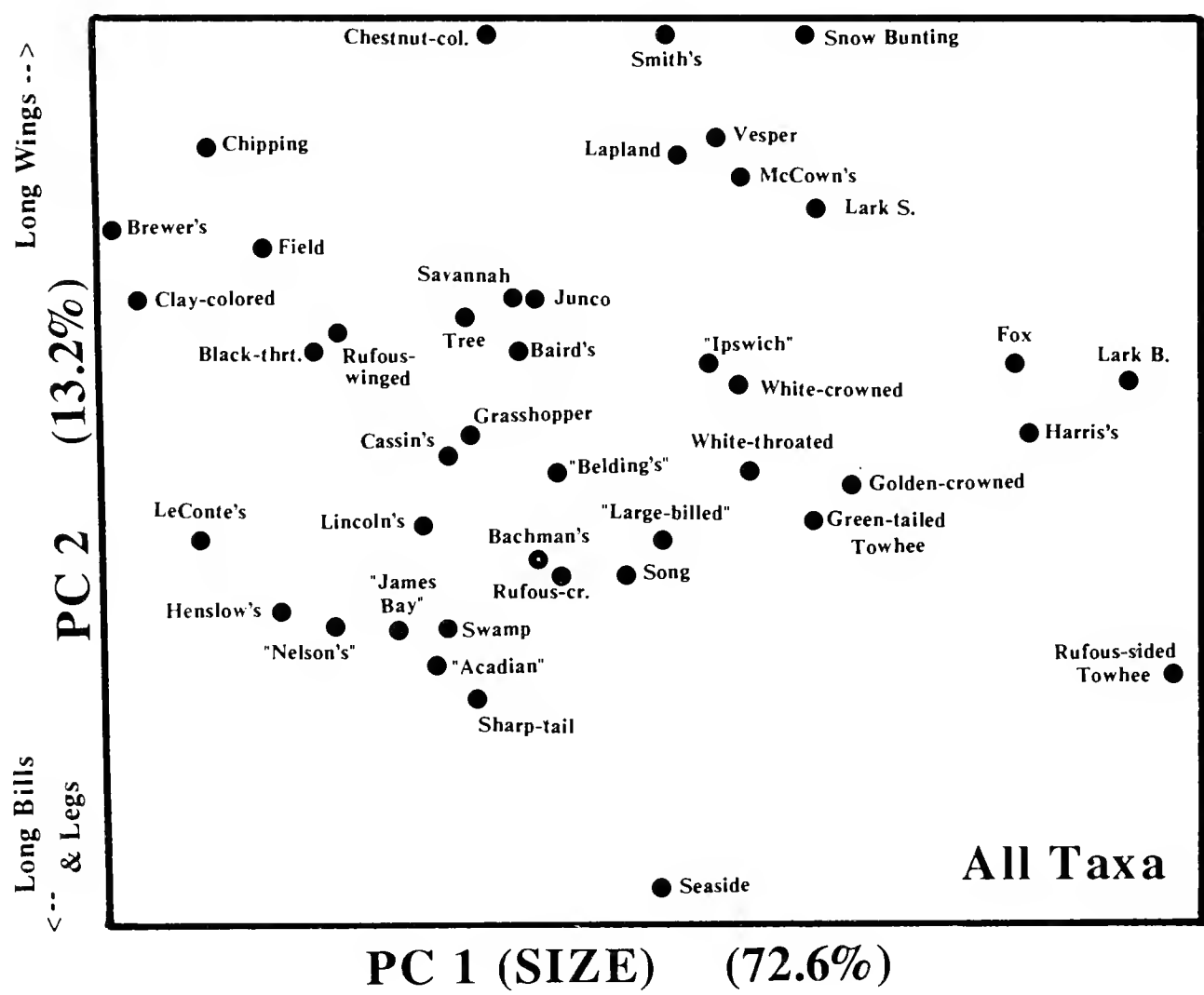


FIGURE 1 – The relationships among four different sets of Emberizids in the space defined by principal components 1 and 2 (PC1 and PC2). The axes are explained in the text.

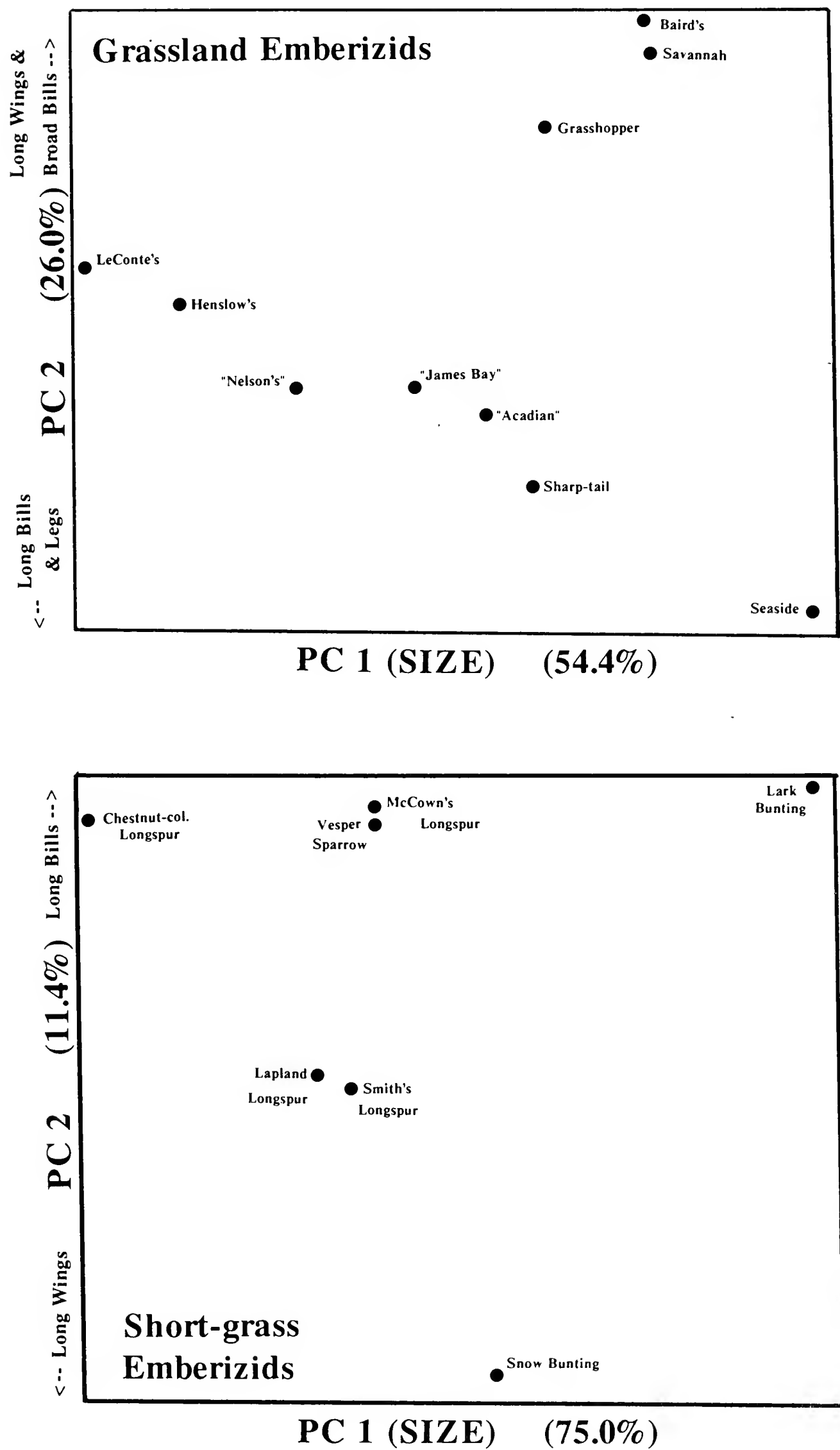


FIGURE 1 – The relationships among four different sets of Emberizids in the space defined by principal components 1 and 2 (PC1 and PC2). The axes are explained in the text.

habitats. These genera are of uncertain relationships, but are often thought to be closely related (Phillips et al. 1964; Mayr & Short 1970; Zink 1982). Although Zink (1982) studied the patterns of genic and morphologic variation among four of these genera (*Passerella*, *Melospiza*, *Zonotrichia* and *Junco*) and Wolf (1977) examined the relationships in the genus *Aimophila* s.s., there has been no phenetic study of representatives of all of these genera taken together.

- (C) The *Pooecetes*, *Calamospiza*, *Calcarius*, and *Plectrophenax* group, seven species that are characteristically found in short-grass prairie or tundra.

RESULTS

Phenetic analyses

The relationship among the 42 taxa of emberizines in the space defined by PC1 vs PC2 is shown in Figure 1. The correlations between the 24 variables and PC1 are all positive and large (Table 2), and thus this axis can be thought of as summarizing size variation among the taxa, with the larger species being to the right of the plot and the smaller ones to the left. PC1 explains 72.6% of all of the variation among the taxa. PC2, which explains an additional 13.2% of the phenetic variation among the taxa, shows substantial positive correlations with ulna, carpometacarpus, sternum and keel length, and sternum depth, and negative correlations with skull, premaxilla, mandible, gonys and hallux lengths (Table 2). This axis, thus, separates the taxa on the basis of shape, with species with relatively long wings (pectoral bone measurements) and short bills and toes toward the top of the figure, and those with relatively long bills and toes, and short wings toward the bottom.

The longspurs *Calcarius* as well as the Snow Bunting, and Vesper and Lark Sparrows, appear together in Figure 1 as species of intermediate size with relatively long wings, short hallux and short bills. The relationships among these species (except for the Lark Sparrow), plus the Lark Bunting (i.e. Group A, Table 2), which is in a monotypic genus that may be close to *Calcarius* (Mayr & Short 1970) and which is also a bird of dry grasslands, are shown in Figure 1. In this plot, PC1 explains 75% of the variability among taxa, and again is best interpreted as a measure of overall size. The PC2 axis, which explains an additional 11.4% of the variation, contrasts bill length with wing length, separating especially the Snow Bunting, which has a relatively short bill and long wings, from the other taxa (Figure 1; Table 2). Of these taxa, McCown's Longspur and the Vesper Sparrow, and Lapland and Smith's Longspurs are very similar in size and proportions.

The sparrows in Group B (Table 2) do not form a discernible cluster in Figure 1, where the relationships among all 42 taxa are shown. Taken by themselves, however, some interesting clusters are evident (Figure 1). The Lark Sparrow is well separated from the others. The *Zonotrichia* cluster together, although Harris' Sparrow is close to the Fox Sparrow on the PC1 (size) axis. Both of these are very large sparrows. (The Fox Sparrow is a highly variable species – and perhaps is several species [Zink 1982]; the birds used here are all representatives of the eastern, *iliaca* group, and not like western Fox Sparrows.) The *Spizella* sparrows likewise fall in the same phenetic cluster.

However, grouped with them are the Dark-eyed Junco as well as the Rufous-winged and Black-throated Sparrows. The latter is the only *Amphispiza* included in this study.

Other than the Rufous-winged Sparrow, the other three *Aimophila* (Bachman's, Cassin's, and Rufous-crowned Sparrows) are close in this phenetic space to the three *Melospiza*.

In the plot (Figure 1) of the "tall grass" and "marsh grass" sparrows (*Ammodramus s.l.* and *Passerculus*), PC1 again is positively correlated with all of the variables and thus can be considered to be a measure of overall size variation among the taxa. However, only 54.4% of the total variance is explained by PC1, and PC2, which explains 26.0% of the variation among taxa, contrasts species with long wings and broad bills with those with long bills and long legs (Figure 1; Table 2). Unlike in the other analyses, the PC2 axis also explains a substantial amount (11.9%) of the total variation; it further divides these sparrows on bill shape, separating Henslow's Sparrow, which has a large, but relatively short bill, from the others. Grasshopper and Seaside Sparrows likewise seem to have proportionally larger and shorter bills than the Savannah Sparrow and their other congeners. The Seaside Sparrow is well separated from the other *Ammodramus*, reflecting its relatively long and narrow bill, short wings and long legs, and large size (Figure 1). LeConte's and Henslow's Sparrows cluster closely together as do Baird's and Savannah Sparrows, which are also close to the Grasshopper Sparrow.

Population Differentiation

The several different populations of both Sharp-tailed and Savannah Sparrows studied here show that within these nominate species there is quite a lot of variability relative to the total variation in the North American Emberizinae.

The Savannah Sparrow is a widespread species that is found in a wide variety of different habitats (Rising 1987). Of the ones studied here, the Ipswich Sparrow breeds only on Sable Island, Nova Scotia, where it is the only regularly breeding passerine. There it is found in heather and dune grass, and not infrequently feeding along the tide line. Belding's and Large-billed Sparrows breed and are resident (for the most part) in intertidal saltmarshes (where *Allenrolfea* and *Salicornia* grow densely) along the coasts of southern California and northern Mexico, and typical Savannah Sparrows (here represented by a sample collected from tall, moist sedge and grass along the coast of James Bay, Ontario) are found in a variety of open-field habitats, including tundra, moist meadows, and pastures with scattered bushes.

The phenetic difference found here among these populations of Savannah Sparrows is comparable, say, to the amount found among the four longspurs (*Calcarius*) plus the Vesper and Lark Sparrow and Snow Bunting, or that within and of the genera studied here. As well the two marsh dwelling populations (Beldings and Large-billed) are more like other marsh-dwelling species (e.g. LeConte's, Sharp-tailed, and Swamp Sparrows) on the PC2 axis, indicating that the relatively long bills and legs of these species represent, in some way, an adaptation to living in marshes.

There is much less phenetic variation among populations of Sharp-tailed Sparrows than Savannah Sparrows, and most of this is along the PC1 (size) axis. Interestingly, the James Bay and Nelson's Sparrows breed in the same habitat (freshwater grass or sedge marshes) (Murray 1969; pers. obs.) and are sympatric with these, whereas the typical Sharp-tailed Sparrows breed in the same habitat (saltmarshes, especially in *Spartina* grass) as Seaside Sparrows, and co-occur with them over much of their range (Woolfenden 1956). All three of these sparrows are apparently closely related

(Zink & Avise 1990), yet Nelson's and James Bay Sparrows are phenetically more like LeConte's Sparrow than are the other Sharp-tailed Sparrows, and typical Sharp-tailed Sparrows are more like Seaside Sparrows than are their other conspecifics. This is not what would be expected if character displacement were occurring, and it indirectly suggests that factors that may lead to it are not important in the evolution of Sharp-tailed Sparrows.

DISCUSSION

Phenetic analyses

I take it as probable that the phenetic differences that I have been able to assess among these taxa tell us more about the ecology of the species than their evolutionary relationships. In any event, some of the results are interesting.

First, in spite of the fact that we are dealing with 42 taxa in 15 generally recognized genera, most of the variability in the group is variability in overall size: about 73% of the variability can be summarized on a single multivariate axis that is highly correlated with each of the 24 characters measured, and over 85% in two multivariate dimensions. The second dimension (PC2) identifies some interesting interspecific patterns of shape variation. The longspurs, Snow Bunting, and Vesper and Lark Sparrows tend to have relatively long wings, a short hallux and short bills. These (perhaps excepting the Lark Sparrow) live in short-grass habitats (at least at some season), or in short tundra habitats where high winds are characteristic. They are also all highly migratory. Although they have relatively short toe bones, they generally have long claws (hence "longspurs"), as is characteristic of birds living in such habitats. The Ipswich Sparrow and Lark Bunting, which are also found in such wind-swept, sparse habitat, however, seem to be "typical" sparrows on the PC2 axis. The marsh-dwelling *Ammodramus* sparrows (Henslow's, LeConte's, Sharp-tailed, Seaside and Swamp) tend to differ from the other taxa studied by having relatively long bills and legs, a long hallux, and relatively short wings. Unlike other sparrows, these seldom fly (although northern and western Sharp-tailed Sparrows have elaborate aerial displays), but do migrate (with the exception of some of the Atlantic coast Sharp-tailed Sparrows). Interestingly, the Swamp Sparrow, which is in the genus *Melospiza* and presumably not closely related to the other marsh-dwelling sparrows, phenetically clusters with these, close to the Sharp-tailed Sparrows, and as mentioned above the two marsh-living populations of Savannah Sparrow studied here are phenetically more like the marsh sparrows than are typical Savannah Sparrows.

For the most part, the species of nominal genera are found together in the various plots, although in general there is no tendency for these groups of congeners to be distinct from all other species in other genera. Thus the *Spizella* sparrows are found together in Figure 1, but the Dark-eyed Junco, and Rufous-winged, Baird's, and Black-throated Sparrows are also included in this "cluster." It is unfortunately true that the reasons for delineating genera in the Emberizinae have not always been clearly stated, and the tendency for congeneric species to cluster together in my phenetic analyses suggests that perhaps general impressions of size and shape have influenced the taxonomy in some undefined manner.

It is interesting that closely-related, sympatric species that live in virtually the same habitats often cluster closely together in our analyses. This is particularly striking among some of the grassland species. For example, the Vesper Sparrow and McCown's Longspur, and Lapland and Smith's Longspurs are extremely close in phenetic space (Figure 1). In the latter case, the range of Smith's Longspur is almost entirely included in that of the Lapland Longspur (which is much more widely distributed), and where the two co-occur they often breed in the same fields (although Smith's seems to prefer somewhat wetter areas than Lapland [pers. obs.]). Likewise the present range of McCown's Longspur essentially falls within that of the Vesper Sparrow, and both species breed in xeric short-grass prairies, although McCown's Longspurs seem to be found in drier and more extensive fields that generally provide territories for Vesper Sparrows, which use fence posts, bushes or trees as singing posts (Godfrey 1986; pers. obs.). Additionally, Baird's and Savannah Sparrows, and to a lesser degree Grasshopper Sparrows consistently cluster closely together. Again, the breeding range of Baird's Sparrow falls within that of the widespread Savannah Sparrow, and the two species commonly breed together in the same fields. Although the Grasshopper Sparrow generally has a more southerly range than these other two species, and is found in drier grassland than either, there are many areas in the northern Great Plains where all three species breed, and breed commonly, in the same fields (pers. obs.). These examples suggest that competition for food or nest sites apparently has not promoted the evolution of phenetic differences of the sort I measured among these species. The Savannah and Tree Sparrows, and Dark-eyed Junco also cluster very closely, and their ranges overlap broadly, but their habitat requirements, especially those of the junco, differ substantially.

LeConte's and Henslow's Sparrows tend to cluster together. These were formerly placed in their own genus (*Passerherbulus*), but Murray (1968) argued that the closest relative of LeConte's Sparrow is the Sharp-tailed Sparrow. Zink & Avise's (1990) clusters of these three species are not conclusive: their MtDNA data place the Seaside and Sharp-tailed Sparrows together, with LeConte's their closest relative, whereas their allozyme data place Sharp-tailed and LeConte's Sparrows together, with the Seaside Sparrow as their nearest relative. As mentioned above, the two populations of Sharp-tailed Sparrows that are phenetically most similar to LeConte's Sparrow breed in same marshes as that species. This is not what would be expected if character displacement were occurring.

The genus *Aimophila* is a complex one that may be polyphyletic, even in the restricted sense that it is generally delimited today. Wolf (1977) recognized three species complexes within this genus, one containing (of the species studied here) Cassin's and Bachman's Sparrows, the second containing the Rufous-crowned Sparrow, and the third containing the Rufous-winged. Phillips et al. (1964) and Mayr & Short (1970) include *Amphispiza* (including the Black-throated Sparrow in this study) in *Aimophila*, but it is not clear within which of Wolf's complexes (if any) they should be put. Our results place the Rufous-winged and Black-throated Sparrows with the *Spizella* sparrows, and close to *Junco* (consistent with Mayr & Short's [1970] suggestion that these three genera are "related"), but place Cassin's, Bachman's and Rufous-crowned Sparrows with the genus *Melospiza* (Figure 1). Our results do not support speculation that the Lark Sparrow is close to *Aimophila* (Mayr & Short 1970).

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CONCLUDING REMARKS: POPULATION DIFFERENTIATION – A 25 YEAR PERSPECTIVE

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ABSTRACT. Over the past quarter century, progress in geographic variation and population differentiation in birds has been made owing to a significant increase in the availability and applicability of multivariate statistics and computers, and to advances in biochemical systematics. The period has also seen advances in research on rapid evolution of introduced species, colonizing species, the niche variation hypothesis, hybridization, central vs. marginal populations, gene flow, subspecific nomenclature, and environmental effects. In the future there may be predicted significant advancement in mtDNA studies, genetic fingerprinting, automation of data gathering, conservation biology, and co-evolution. Within the profession there is concern for museum collections, training of systematists, and funding.
Keywords: History, multivariate statistics, biochemical systematics. methods, theory.

INTRODUCTION

Many evolutionary biologists consider speciation the important event: geographic variation is mere foreplay. In fact, exploring the nuances of variation among populations makes understanding the speciation event more deeply satisfying. The study of patterns of population differentiation puts one close to the process of evolution.

Ornithologists were once in a pre-eminent position in evolutionary biology (Mayr's 1963). This seems not to be the case today. As evolutionary biology moved over the last two decades from the field and research collection to the laboratory, birds were not the animals of choice. As the focus shifted from phenetics to genetics, birds did not show variation in the characters to be measured. That may be changing.

A 25 year perspective on geographic variation requires mention of multivariate statistics, and computers, and biochemical systematics. These tools have been very important to the field (Gould and Johnston, 1972; Zink and van Remsen 1986; Barrowclough in this symposium). In addition, there are a number of theories, special areas of inquiry, and expectations I had for the field a quarter of a century ago that are interesting to consider in perspective.

EXPECTATIONS

Methods

MULTIVARIATE STATISTICS AND THE COMPUTER REVOLUTION. Multivariate statistics appeared on the scene in the early 1960s. Known primarily to statisticians, up to that time they had been applied in biology only by laborious machine calculations on a handful of characters (Jameson et al. 1966, Jolicoeur 1959). My work on Red-winged Blackbirds *Agelaius phoeniceus*, reported at an AOU meeting in Toronto in 1967, may have been

the first application of canonical variates analysis to geographic variation of birds. As much time went into writing the computer programs as it did in analysing the data.

Use of multivariate statistics has grown significantly, facilitated largely by the availability of computer programs. Computers were not available prior to the 1960s. Even using them in the mid-60s often required writing programs in Fortran, an additional language requirement which thwarted many. Statistical packages such as BMDP, SPSS, and SAS changed that: sophisticated statistics could now be bought, but by the computer centre, not the individual. Statistical packages were expensive to purchase and maintain. It was clear that the computer needed to move from the computer centre to the office. First came terminals with which one could dial into a mainframe. Now, complex, multivariate statistics can be done at desks using personal computers and packages such as Systat. Change has been primarily in availability and in familiarity.

Many methods are still scarcely past their infancy: their theoretical development and underlying justification not fully worked out (Oxnard 1978). There also have been a number of multivariate approaches that have not caught on, such as Bookstein's (1982) "tensor method."

BIOCHEMICAL SYSTEMATICS. Studies in the 1960s using gel electrophoresis of protein of egg white, serum, and other tissues provided little insight into population differentiation. In the 1970s DNA-DNA hybridization took us closer to the genome but, still, birds did not vary enough within species for those techniques to be insightful. The tool of the future came along when maternally inherited, extranuclear, mitochondrial DNA (mtDNA) proved variable within species (Shields and Helm-Bychowski 1988; Moritz et al. 1987). Now, DNA fingerprinting allows study even of parentage (Burke 1989).

GENETIC AND PHENETIC COVARIATION. One of the great disappointments has been the failure of geographic variation and structure of population differentiation in biochemical characters to match that of morphological characters (Barrowclough 1980, 1983; Capparella & Lanyon 1985). However, this development did lead to consideration of neutral selection for genes coding for proteins. It also brought into question the level of genetic variation and heritability of many of the morphological traits that were being used. Covariation between genetic and phenetic components has yet to be resolved (Hillis 1987).

Theory

RAPID EVOLUTION OF INTRODUCED SPECIES. A profound paper in 1964 was one that reported evidence for rapid evolution of morphological traits. Johnston and Selander (1964) studied geographic variation of the introduced House Sparrow *Passer domesticus* in North America and found that variation recognizable at the subspecies level occurred within 100 years of the date of introduction. This gave insight into the success of efficient colonisers as well as into the plasticity of morphological traits we had come to rely on for describing subspecies and investigating clinal size and colour variation of the type predicted by Bergmann's and Golger's rules.

COLONIZING SPECIES. Stimulated by Johnston and Selander's work, there has been study of introduced and colonizing species elsewhere. Baker and Dennison have given a good summary in this symposium. There is still excitement about the evolution of

colonizing species, and there is still much to learn about the rapidity of phenetic and genetic change, and especially about the evolution of variability.

THE NICHE VARIATION HYPOTHESIS. An area in which I would have expected something more definitive over the last 25 years is the niche variation hypothesis. Van Valen (1965) piqued interest in the possibility that populations are more variable in a broader niche or fluctuating environments. Lamentably, there has been little satisfaction with phenotypic approaches to the study of geographic variation in variability (Power 1983). Museum skins collected over time, or even populations collected at a single point in time, are subject to too much extraneous variation. The future for some connection between variability and the environment seems to lie with studies of genetic, not phenetic, attributes (Hedrick 1986).

HYBRIDIZATION. Analysis of hybrid zones remains high on the list of interesting topics (Barrowclough 1980, Rising 1983, Short et al. 1983). Documenting and understanding hybridization requires analysis of clinal variation in the two interbreeding species, both outside and in the hybridization zone (Barton & Hewitt 1985).

CENTRAL V MARGINAL POPULATIONS. Ever since Gould and Eldredge (1977) advocated punctuated equilibria over gradual differentiation in the speciation process, we have been more aware of the differences in variation in central vs. marginal populations. The central-marginal model asserts that populations near the centre of a species' range usually display high levels of genetic and phenetic variation, while populations at the margins are more monomorphic (Lewontin 1974, Mayr 1963). My own studies (Power 1980) on differentiation of California Islands populations of the House Finch *Carpodacus mexicanus* and Rock Wren *Salpinctes obsoletus* in comparison with geographic variation on the adjacent mainland suggested peripheral isolates are most likely to diverge into new species. Describing geographic variation in the centre vs. margins of a species range remains a fruitful area of research on speciation.

GENE FLOW. In the 1960s, Mayr (1963) had been a principal advocate for a conservative effect: gene flow is important in maintaining homogeneity in a species. Then came the exciting challenge from Ehrlich and Raven (1969), and later from Endler (1977), that genes may not be flowing very much owing to limitations of dispersal and the forces of natural selection at the population level. Slatkin (1985) sees evidence that under "normal" conditions gene flow may be restricted, but under other conditions, particularly those that cause large-scale demographic changes, gene flow over long distances "will occur; ". . . gene flow resulting from the extinction and recolonization of local populations may be the principal mechanism of gene flow" (p. 394). It is time for another reappraisal of gene flow. The new biochemical methods, especially mtDNA analysis, can provide gene frequency data. Coupled with direct observations of dispersal, these will yield insight into demographic properties of populations. Perhaps such studies should be initiated on islands.

SUBSPECIES. Earlier (Power 1970) I advocated that subspecies names should not be used. I believed trinomial taxonomy concealed the true nature of geographic variation: subspecies names oversimplified reality and often implied boundaries where none existed, except in the case of geographic barriers to breeding, and, then, why could not the subspecies meet the definition of a full species in the Mayrian sense. I have come about 180 degrees. The subspecies concept still has all of the old problems, but

trinomials have given us an edge in arguing for the preservation of endangered species. We can argue with politicians and developers about saving, say, the Northern Spotted Owl *Strix occidentalis caurina*, noting it is a unique *kind*, even though it is in fact an intraspecific differentiate.

ENVIRONMENTAL EFFECTS. In the early 1980s James (1983) conducted astounding research. She seemed to demonstrate that Red-winged Blackbirds raised outside their specific breeding locality took on the characteristics of the population in which they were raised. This was a classic experiment demonstrating the environmental component of phenotype. The findings have profound implications for all studies of within-species variation in morphological traits. It is surprising that there have not been more studies in this important area.

PROJECTIONS

Continuing research

MTDNA. Over the next 25 years there will continue to be significant advances in the use of mtDNA in population differentiation. This in turn will lead to a greater understanding of many of the evolutionary concepts developed in the past.

GENETIC FINGERPRINTING. Understanding relatedness and knowing parentage is already having a great impact on behavioural ecology. Genetic fingerprinting will play an important role in understanding the mechanics of population differentiation as well.

AUTOMATION OF DATA GATHERING. We must keep an eye on engineering, electronics and optics. Developments may be made in stereology, image analysis, computer graphics, pattern recognition and other areas mediated by computer science and electrical engineering. These will not only help in rapidly gathering and classifying traditional morphological data, but open new inroads into analysing complex data such as plumage patterns, skull shape, and totally new kinds of physical characters.

CONSERVATION BIOLOGY. The service of systematists to conservation biology is unquestioned. Daugherty and Triggs, in this symposium, address the studies of endangered New Zealand species and it is clear that without studies of geographic variation we would not know what populations have differentiated and are in need of protection. *Species listed as endangered or threatened ought to be top priority for study.*

CO-EVOLVING SPECIES. Much can be done with the geographic variation of interacting species. Rising, in this symposium, has reported similar variation according to habitat type within emberizines. We know about character displacement: the effect where two potentially competing species are more dissimilar where their ranges overlap than where they do not. However, some supposed character displacement may disappear when the entire range of geographic variation is examined: the trend may be the results of natural selection by the environment. New areas of research may involve covariation of hosts and parasites, predators and prey, or even members of widely ranging communities of species that tend to occur together. Are there cases when the interactions among species mediate or enhance geographic variation?

The profession

MUSEUM COLLECTIONS. Being a museum director, I worry about what will become of museum collections. With emphasis being placed on biochemical methods, will museums' vast collections become even less used than now? I am optimistic they will not. With a focus on endangered and threatened species, and with concern amount diminishing biodiversity in critical habitats, systematic collections will continue to have value. The question is an important one, though, for planning or funding expansion and modernization of research collections.

TRAINING OF SYSTEMATISTS. Universities are hiring fewer faculty trained in or conducting whole-animal and habitat-oriented research, continuing a trend that has been going on for at least two decades. Organismic biology may soon come to reside in museums or government agencies concerned with management of wildlife resources.

FUNDING. Certain research, like the Human Genome Project, can draw large sums of government money. Avian systematics has not been in that company. However, history reveals at least one successful connection between federal funding and the study of intraspecific variation that may provide a lesson. The French ethnologist Armand de Quatrefages was incensed by the damage done to Paris' Natural History Museum by German shells during the Franco-Prussian War of 1879. He declared that the Prussians were by race not Nordic or Teutonic but descendants of the barbarian hordes of Huns who ravished eastern Europe during the Middle Ages. Rudolf Virchow, a German pathologist and politician, was outraged by this racial slur. As a member of the Prussian Parliament, he introduced a bill by which the physical characteristics of every schoolchild in Prussia – six million in number – could be examined and assessed. The survey was carried out, head measurements, bones, hair, and teeth were all analysed, and Virchow proved morphometrically that the Prussians were in origin Franks-cousins, in fact, of the French themselves.

What do you think the reaction of New Zealand's parliament might be if a resolution were passed at this Congress that the Kiwi was nothing more than a diminutive flightless ratite and that much of New Zealand's avifauna is truly deviant? Perhaps we in the United States can expect an outpouring of government funds too if you return the favour by labelling the American symbol, the Bald Eagle *Haliaeetus leucocephalus*, little more than a scavenging, oafish Buteo.

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SYMPOSIUM 6

**THE METHODOLOGY OF RECONSTRUCTING
THE PAST**

Conveners A. ANDORS and F. VUILLEMIER

SYMPOSIUM 6

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INTRODUCTORY REMARKS: THE METHODOLOGY OF RECONSTRUCTING THE PAST

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Like the fossil birds that this part of the Congress programme treats, Symposium 6, "The methodology of reconstructing the past", has had a chequered history. This symposium was originally conceived as a series of case studies in Southern Hemisphere avian paleontology, each using a different methodology, but all being aimed at the common goal of reconstructing either extinct taxa or genealogies or faunas. The methodologies were to include DNA sequencing, paleoimmunology, sedimentology, morphology, avifaunal comparisons, and artistic reconstruction. Unfortunately, these original plans could not be carried out. Symposium 6 was for a time cancelled (due to the withdrawal of its original convenors and some intended participants), then resurrected in its present form with two new convenors, three new speakers, a different schedule, an amended title, and a purview that now extended into the Northern Hemisphere. This reincarnated symposium bears scant resemblance to its defunct predecessor. However, it does retain much of the same methodological diversity, and we trust that it also retains all of the interest and relevance of the symposium that was originally intended.

Two of the papers contained herein (Andors; Peters) are northern in emphasis; the others (Worthy; Vuilleumier & Kikkawa) treat southern taxa. (A fifth contribution presented by A. Cooper at the symposium in Christchurch, will be published elsewhere. It deals with molecular methodologies and southern taxa.) The four reports exemplify methodologies (including morphological and faunistic approaches) that are widely employed in avian paleontology, including other paleontological contributions to this Congress. However, we hasten to add that they comprise only a small sample of present-day approaches. For overviews of recent work in avian paleontology, we commend to the reader the three Festschriften honoring the seminal work of Alexander Wetmore (published in 1976), Hildegard Howard (1980), and Pierce Brodkorb (in press). The last is the second of a series of quadrennial international symposia sponsored by the Society of Avian Paleontology and Evolution (SAPE). Founded in 1985, the SAPE is the world's only organization devoted solely to the advancement of knowledge of avian paleontology.

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MOLECULAR STUDIES OF NEW ZEALAND'S EXTINCT RATITES.

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ABSTRACT. DNA was isolated from mummified remains of moas representing 5 genera (*Megalapteryx*, *Anomalopteryx*, *Pachyornis*, *Dinornis* and *Emeus*). The extracted DNA allowed enzymatic amplification of small pieces of mitochondrial genes from each genus. The nucleotide sequences of a 400-base pair segment of the mitochondrial gene for the 12S-ribosomal RNA were determined. Bone from a *Megalapteryx* specimen was found to be a source of DNA as well as skin and muscle remains. The implications of such ancient DNA studies are discussed.

Keywords: Ancient DNA, ratite birds, moas, 12S gene, polymerase chain reaction, DNA sequencing.

AN OVERVIEW OF THE TAXONOMY, FOSSIL HISTORY, BIOLOGY AND EXTINCTION OF MOAS

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ABSTRACT. Eleven moa species (Dinornithiformes: Dinornithidae, Emeidae) are recognized, dating back to about 2.4 myBP. These ranged in mass from about 15-270 kg. Some moas showed marked sexual size dimorphism. In others size decreased from the colder last Glacial to the warmer Holocene. Evidence on diet for 4 species shows that moas were browsers and ate twigs, leaves, and fruit. Species were spatially separated by preference for 1 of 3 habitat types: wet dense lowland forest; drier mosaics of grassland, shrubland, and forest; upland/subalpine areas. Size and bill morphology restricted the food available to taxa and minimized competition between them. The only inferred predator upon adult moas was the huge Haast's Eagle. Its minor predatory impact and the predictable environment probably resulted in the moas having had a low reproductive potential. Thus, notwithstanding the survival of moa species into the Holocene, all were extinct about 600 yr after man arrived in New Zealand. A combination of habitat modification and overkill caused their extinction.

Keywords: Moas, Dinornithiformes, classification, biology, ecology, extinction, fossil birds.

INTRODUCTION

Moas were first noticed by the scientific community when Owen (1840) described a fragment of a femur. His controversial deduction that the bone was from a bird was soon vindicated: by 1843 he was able to describe the bones of 5 species (Owen 1846). This taxonomic diversity and the stupendous size of some species impressed Owen. Amongst his conclusions was the assertion that moas were closest to cassowaries and thus by analogy *D. giganteus* was no more than 10 feet tall. He noted that moas were probably vegetarian (because all known struthious birds were) and related their amazing diversity to the absence of mammals in New Zealand. By 1848 he had described nine species including seven of the 11 accepted here.

Over 150 years have elapsed since the first moa bone was described. What were moas? What do we know of their biology or their history after a century and a half of investigation? Some answers to these questions are given in this contribution.

CLASSIFICATION AND DISTRIBUTION

For most of the last century and a half the species diversity of moas has been overestimated. Anderson (1989) provides lists of the classifications applied in the past. The classifications used more than any others are those given in Archey's (1941) and Oliver's (1949) monographs. They recognized 20 and 29 species respectively. Recent morphological studies of bones have supported the concept that there were only 11 moa species in two families (Dinornithidae, Emeidae; Table 1) (Cracraft 1976, Millener 1982, Worthy 1988a,b, 1989a). In the monotypic family Dinornithidae, three species are recognized in the genus *Dinornis*. Dinornithids were tall and, among moas,

TABLE 1 - A classification of the moas (Aves: Dinornithiformes) showing the distribution of species in New Zealand (NI = North Island; SI = South Island; * = endemic to one island).

Family	Subfamily	Genus	Species	Distribution
Dinornithidae		<i>Dinornis</i>	<i>giganteus</i>	NI, SI
			<i>novaezealandiae</i>	NI, SI
			<i>struthoides</i>	NI, SI
Emeidae	Emeinae	<i>Euryapteryx</i>	<i>curtus</i>	NI *
			<i>geranoides</i>	NI, SI
	Anomalopteryginae	<i>Emeus</i>	<i>crassus</i>	SI *
		<i>Anomalopteryx</i>	<i>didiformis</i>	NI, SI
			<i>mappini</i>	NI *
		<i>Pachyornis</i>	<i>elephantopus</i>	SI *
			<i>australis</i>	SI *
			<i>didinus</i>	SI *
		<i>Megalapteryx</i>		

relatively gracile. Among other characters, dinornithids can be diagnosed by their broad, flat crania with down-curved bills, 29 or 30 presacral vertebrae, and tarsometatarsus longer than femur, which itself was half the length of the tibiotarsus.

Moas placed in the family Emeidae were usually shorter and were characterized by 27 presacral vertebrae, rounded crania whose depth was greater than half the width, and a tarsometatarsus shorter than the femur, which itself was more than half the length of the tibiotarsus. Two subfamilies of emeids are recognised. The Emeinae (Archey 1941) can be diagnosed by the phalangeal formula 2:3:4:4 with digit 1 very reduced; a foreshortened rounded bill; a reduced gizzard; an extensive tracheal loop; and an absence of coracoidal grooves on the sternum. The Anomalopteryginae Archey 1941 had, by contrast, a phalangeal formula of 2:3:4:5 with digit 1 prominent; a pointed bill; a normal gizzard; no tracheal loop; and prominent coracoidal grooves on the sternum (except in *Pachyornis elephantopus* (Owen)).

Of these 11 species in 2 families, 7 (2 endemic) occurred in the North Island and 9 (4 endemic) in the South Island. The three species of *Dinornis* (Dinornithidae) occurred on both the North and South Islands. The six endemic species are all in the Emeidae, one in *Euryapteryx* (North Island), one in *Emeus* (South Island), three in *Pachyornis* (one North Island; two South Island), and one in *Megalapteryx* (South Island).

FOSSIL HISTORY OF MOAS

New Zealand has a dearth of fossiliferous terrestrial deposits (Fleming 1979), and almost no fossil record of terrestrial vertebrates earlier than the Quaternary. Despite this incomplete record, a recent review of the fossil material older than the Otira (last) Glaciation (Worthy et al., in press) has revealed 40 records or specimens of fossil moa bones thought to be older than 75,000 years but no older than 2.5 m yr. Fifteen records are temporally unprovenanced, leaving 11 Haweran (75 to 400 k yr BP), 8 Castlecliffian (400 k yr to just over 1 m yr BP), and 6 Nukumaruan (about 1 to 2.4 m yr) records. The oldest fauna (Nukumaruan) included *Dinornis novaezealandiae*

(Owen), *Euryapteryx curtus* (Owen), *E. geranoides* (Owen) and possibly *Anomalopteryx didiformis* (Owen).

This early Pleistocene taxonomic diversity suggests that moa speciation was not a result of, nor much affected by, the Pleistocene ice ages. It can be suggested, furthermore, that all species known from the Holocene were probably already present before these events. The presence of typical *Euryapteryx* bones of both species, about 2.2 m yr old, shows that the subfamily Emeinae, considered by some authors to be the most derived moas, had diverged from other emeids before then. The history of moas as a distinct group of birds can therefore be expected to extend several million years earlier than that. The available fossil evidence supports neither the Gondwanan ancestry of moas (Cracraft 1974), nor hypotheses centered about more recent ancestry from volant immigrants (Houde 1986).

SIZE VARIATION

In the past the taxonomy of moas has, to a large extent, been based on measurements of bones. Species limits were set without proper consideration of biological variability. Because moas were of large size some researchers, for example Hutton (1892), perceived the range of size variation now accepted within a single species, to be unacceptably large and so they imposed narrow size limits to define species. The relationship of size variation to absolute size was not examined until Cracraft (1976) looked for normal size variation in leg bones. Among the then accepted moa species he identified several pairs of species which were considered to represent just one in each instance. For example the bones referred to the species pairs *Emeus crassus* / *E. huttoni* and *Pachyornis mappini* / *P. septentrionalis* were demonstrated to be referable to just one taxon in each instance (that listed first here). Since Cracraft's (1976) work I have examined moas of all species in detail and can define the leg and cranial bones of all emeids using primarily shape characters (Worthy 1988b). The classification in Table 1 is prepared on this basis. The size variation of leg bones of taxa so defined is described by coefficients of variation (CVs) in the range of 3 to 10.

Higher CV values may result from lack of control of geographic and temporal variation. There is good evidence that some species decreased in mean size from the last glacial (Otira 25 to 14 kyBP) to the Holocene (<10 kyBP), for example *Pachyornis mappini* and *Euryapteryx curtus* (Worthy 1987), and *Megalapteryx didinus* (Worthy 1988a). Bones of *Euryapteryx geranoides* increase clinally in size from north to south (Worthy 1988b).

Size variation is also related to sexual dimorphism in at least three species, *E. curtus*, *P. mappini* and *Emeus crassus* (Cracraft 1976, Worthy 1987). Sexual dimorphism in size probably was not present, or if present was certainly not marked, in *Megalapteryx didinus* (Worthy 1988a), *Pachyornis australis* (Worthy 1989a), *Anomalopteryx didiformis* and the three *Dinornis* species (Worthy 1989e). The coefficients of variation in bone length of sexually dimorphic moa species range from 8 to 10. Kiwis, like most ratites, are known to be sexually dimorphic in size with females larger. However, Figure 7 in Worthy (1987) shows the size distribution of long bones, at least in *Apteryx australis mantelli*, to be unimodal. The size ranges of the two sexes overlap too much

to produce a bimodal distribution. A sample of 30 Brown Kiwi skeletons from the National Museum of New Zealand gave CVs of 6.79, 6.97 and 6.40 for femoral, tibiotarsal and tarsometatarsal lengths, respectively (unpublished data). The higher CV values for some moa species reflects marked bimodality in size distribution on a scale similar to that described for the strongly sexually dimorphic European cave bear *Ursus spelaeus* (Kurten & Werdelin 1990).

SIZE OF MOAS

Moas are often thought of as huge birds. Some were: the largest *Dinornis* probably exceeded 272 kg (Atkinson & Greenwood 1989), but intraspecific size range was large. Nevertheless six taxa probably regularly exceeded 100 kg, the approximate weight of an ostrich (*Struthio*). Atkinson & Greenwood (1989) found that in each species the calculated weight of the largest individual was approximately double that of the smallest individual measured, a not unusual phenomenon in birds. They listed *M. didinus* as the lightest moa with a minimum weight of about 17 kg, but Holocene-aged individuals of both *E. curtus* and *P. mappini* were often lighter than this, judging from their bone size. Weights for these taxa were not determined by these authors.

HABITAT AND DIET

Early workers assumed that moas were vegetarian because they believed all living struthious birds are. Owen (1844) thought that some moas ate fern roots. Their size and robustness led Haast (1872) to promote the idea of moas being grassland birds. However, evidence of diet was only discovered 20 years later (Hamilton 1892), when gizzards of about 2 kg and 2.7 kg weight were described. These contained masses of *Leucopogon* and *Coprosma* seeds, and twigs. This gizzard size is typical of those associated with larger moa species in more recent finds. Despite these observations, and those of gizzard contents of Pyramid Valley moas (Falla 1941), the notion of grassland moas prevailed. However, the evidence (Gregg 1972, Burrows 1980) eventually convinced people that moas, more specifically *Dinornis giganteus*, *D. struthoides*, *Emeus* and *Euryapteryx*, were browsing birds. Species of *Dinornis* included many twigs in their diet, but *Emeus* and *Euryapteryx* apparently were restricted to softer leaves and fruit. At present there is no evidence about the diet of *D. novaezealandiae*, *A. didiformis*, *M. didinus*, *E. curtus*, or any species of *Pachyornis*.

During most of the Holocene, New Zealand was nearly entirely forested. Grasslands occurred only in subalpine areas, in the driest areas east of the main ranges in the South Island, and on the mobile surfaces of dunes or riverbeds. However, although the term forest describes most habitats, some significant distinctions can be made within the category. The lowland areas of the North Island and western areas of the South Island were cloaked in tall, dense, wet, mixed podocarp forests. Upland areas were often dominated by relatively open beech forests. Large areas east of the Southern Alps were in the rain shadow zone and presented a mosaic of tall and low forest, shrubland, and grassland of a drier, and probably more open, nature than western or northern areas. Similarly, coastal dunes probably supported mosaics of grasslands, shrublands and forest.

An analysis of moa species distribution and species frequency within sites has revealed three distinct assemblages (Worthy 1990).

1. The *Anomalopteryx* assemblage — *A. didiformis* and *D. novaezealandiae* predominate in deposits laid down when tall, dense, wet, lowland mixed podocarp forests prevailed. *Pachyornis* and *Euryapteryx* species are rare in such deposits.
2. The *Euryapteryx* assemblage — In most North Island dune deposits, the smaller *E. curtus* is the predominant species, with frequent *P. mappini* or *D. giganteus* or *D. struthoides*. In the southwest North Island dune deposits *E. geranoides* dominates. In eastern lowland areas of the South Island *E. geranoides* is codominant with *Emeus crassus*, although there is evidence the latter species preferred areas below 200 m above sea level and *E. geranoides* higher areas (Worthy 1990). Other common species were *P. elephantopus* and *D. giganteus*.
3. The upland - subalpine assemblage — The subalpine areas were utilized, if only seasonally, by four species of moa (Worthy 1989b). The predominant species was *Megalapteryx didinus*; other species were *Pachyornis australis*, *D. novaezealandiae* and *D. struthoides*. *M. didinus* was probably an upland specialist: the largest accumulations of its bones are all from subalpine areas. It was the only species of moa known to have had feathered tarsi.

INTERSPECIFIC DIFFERENCES AFFECTING FEEDING AMONG MOAS

Some of the morphological differences between taxa of moa probably helped to reduce competition between species. Atkinson and Greenwood (1989) examined differences in height, bill, and gizzard structure which are directly related to feeding.

Height

In each moa genus the constituent species have a size range that does not overlap with that of congeners to any extent. One may infer from this that size differences probably reduced interspecific competition. Competition between dinornithids and emeids may have been lessened by the greater stature of dinornithids. All dinornithids were taller than emeids of equal weight because of their relatively longer legs and three additional mid-cervical vertebrae (Worthy 1989c). Also, the two larger dinornithids *D. novaezealandiae* and *D. giganteus* were taller than any emeid.

Bill morphology

Bills of the three dinornithids were similar, and different from those of emeids. Among emeids there are two principal types of bills: sharp and pointed, and blunt and rounded. The sharp bills of *Pachyornis* and *Anomalopteryx* were very robust, whereas that of *Megalapteryx* was comparatively weak. The blunt bills of *Euryapteryx* and *Emeus* species were the weakest of all moas and were also very short.

Gizzards and diet

Gizzard analyses have shown that *Dinornis* had relatively large gizzards with large stones and that the preferred diet was twigs (Burrows et al. 1981). The short blunt bills of emeine species were associated with gizzards of small volume that contained relatively small stones. Worthy (1989d) suggested that these taxa preferred soft foods

such as fruit and softer foliage. This idea is corroborated by the few gizzard analyses available for these taxa. The pointed, generally robust bills of Anomalopteryginae suggest that their preferred diet was different from that of Emeinae. The large volume of the gizzard and large gizzard stones of *A. didiformis* suggest that this species was adapted to a fibrous diet. It is expected that *Pachyornis* would have had similar preferences but that *Megalapteryx*, with a weaker bill, ate different items.

From their distribution, we can surmise that coarse habitat preferences separated the anomalopterygine taxa. *P. australis* was bigger and had a considerably more robust bill than *M. didinus*, indicating that food preferences reduced competition between these taxa, the only two Anomalopteryginae known to have been largely sympatric. Some overlap could be expected at ecotones as shown on an altitudinal gradient from *M. didinus* (subalpine) to *A. didiformis* (lowland, wet) (Worthy 1990). Thus differences in bill and gizzard morphology among families or subfamilies, height or size differences occurring mainly within genera, and habitat preferences among species, served to reduce competition among moa taxa.

PREDATORS

As Owen noted long ago, New Zealand was devoid of terrestrial mammals before the advent of man. Although moas did not have to contend with mammalian predators, there were avian predators. Haast's Eagle (*Harpagornis moorei* Haast) was the world's largest eagle, with a wingspan of over 2.5 m; large females may have reached 13 kg (Holdaway 1989). Haast's Eagle was a good flier and, with its weight and huge talons spread, it could easily have killed many of the moa species. Haast's Eagle coexisted with moas in subalpine and other areas where relatively open habitat is postulated to have prevailed, for example east of the Southern Alps during the Holocene. Other avian predators were considerably smaller; the extinct harrier *Circus eylesi* weighed only about 1.2 kg and the falcon *Falco novaeseelandiae* was even smaller. These birds cannot have been much of a threat to adult moas but probably preyed on moa chicks. The role of the enigmatic gruiform *Aptornis otidiformis* Owen in New Zealand's prehuman ecosystem is unknown, but its stout bill morphology suggests that it may have been an effective predator of small animals, and it could have taken moa eggs.

BIOLOGICAL QUIRKS AND EXTINCTION

Moas existed in a relatively stable, predictable environment during the Holocene. The major predator they had to contend with was restricted to areas with forest edges, or to areas with low and more open forest. These characteristics of the moas' environment probably meant that these birds were long-lived and had low reproductive capacity. Anderson (1989), estimating the biomass of moas, using emus as an analogy, concluded that the standing crop of moas, for all species combined, was probably less than 100,000 individuals for all of New Zealand. This scenario of low population density should be considered in conjunction with the concept that each species had its preferred habitat. Thus during the Holocene the *Euryapteryx* assemblage, in the North Island, had only a very restricted area of prime habitat available, whereas the *Anomalopteryx* assemblage had available most of the North Island. These eco-geographic factors contributed to the extinction of the moas. Man arrived in New Zealand

about 1000 years ago. The analogy derived from observations of emu populations suggests that the densest moa populations lived in the drier zones or areas of shrubland/grassland/forest mosaics. These areas are shown by archaeological evidence to have been those most used for hunting (Anderson 1989). Such ecotonal areas were probably easier to hunt in than more uniform habitat, and were also more prone to habitat change by burning. Moas ceased to be of economic significance to the Maori by 300-400 years ago. Whatever the hunting method employed, after 600 years of human occupation moas were extinct in most regions of New Zealand. There are no well documented claims of moa sightings by Europeans (Anderson 1989). Excessive hunting pressure combined with habitat change caused the extinction of the spectacular moas along with that of over 20 other land birds (Atkinson 1989).

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PALEOBIOLOGY AND RELATIONSHIPS OF THE GIANT GROUNDBIRD *DIATRYMA* (AVES: GASTORNITHIFORMES)

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ABSTRACT. Fossils of the giant, flightless groundbird *Diatryma* are known from the Eocene of North America and Europe. The disjunct distribution of *Diatryma* is attributable to an episode of trans-Atlantic dispersal across a northern terrestrial corridor in the Early Eocene. Pelvic limb features indicate a close affinity between *Diatryma* and the Old World *Gastornis*; both genera are placed in the order Gastornithiformes. Cranial and postcranial characters suggest that the Gastornithiformes are related to the Anseriformes and, more distantly, to the Galliformes, not to the Gruiformes as commonly believed. Contrary to the view of gastornithiforms as cursorial predators, it is argued that *Diatryma* was primarily herbivorous and pedestrian in gait. Its nonflying wing is interpreted as having been reduced distally in association with evolutionary increase in body size. Depositional environments indicate that *Diatryma* inhabited well-vegetated coastal lowlands and alluvial floodplains, much as its presumed close relatives, the Neotropical Anhimidae (Anseriformes).

Keywords: *Diatryma*, Diatrymidae, Gastornithiformes, Anseriformes, fossil birds, paleobiology, phylogeny, evolution.

INTRODUCTION

The presence of giant groundbirds in the lower Tertiary of Europe and North America was first noted by Hébert (1855a,b), who described an avian femur and tibiotarsus from the Lower Eocene (Sparnacian) of France as *Gastornis parisiensis*, and by Cope (1876,1877), who described a fragmentary tarsometatarsus from contemporaneous (Wasatchian) deposits in New Mexico as the type of *Diatryma gigantea*. Hébert and others regarded *Gastornis* as a relative of waterfowl (Anseriformes), whereas Cope considered *Diatryma* and *Gastornis* to be Northern Hemisphere representatives of the ratites (Palaeognathae). Cope also believed that *Gastornis* and *Diatryma* were related *inter se*, and that the two genera were useful in stratigraphic correlation. Stejneger (1885) erected a ratite order Gastornithes (= Gastornithiformes) for *Gastornis*, *Diatryma*, and various putative relatives. Coues (1884) proposed synonymizing *Diatryma* with *Gastornis*, but an affinity between these genera was disputed by Matthew & Granger (1917). Subsequent authorities placed *Gastornis* and *Diatryma* in separate families (Gastornithidae, Diatrymidae) in the same or in different orders (Gastornithiformes, Diatrymiformes). For reasons given below, gastornithids and diatrymids are referred to henceforth as gastornithiforms.

Considerable additional gastornithiform material has come to light since *Gastornis* and *Diatryma* were discovered. Diatrymids have been recovered from the Lower Eocene (Wasatchian/Ypresian) of New Mexico, Colorado, Wyoming, New Jersey, Ellesmere Island and France, and from the Middle Eocene (Geiseltalian/Lutetian) of Germany. More than 50 specimens of *Diatryma* are now known from North America (Andors 1988). Collections of diatrymids from North America include several geographic range extensions (in Wyoming and Colorado) and several elements not previously noted

(ulna, carpometacarpus, metatarsal I). Gastornithids (*Gastornis* spp.) have been found in the upper middle Paleocene of East Germany, in the Upper Paleocene (Thanetian/Cernaysian) of Belgium and France, and in the Lower Eocene (Spartan) of England and France. A second genus of gastornithid, *Zhongyuanus*, has been reported from the Lower Eocene of China (Hou 1980). The geochronologic ranges of the Gastornithidae and Diatrymidae (Figure 1) overlap in the Early Eocene, with Paleocene - Eocene gastornithids ultimately being “replaced” by Eocene diatrymids. The apparent replacement may be a taxonomic artifact if, as has been suggested (Martin 1983, Andors 1988), the family Diatrymidae Shufeldt 1913 is a junior synonym of the Gastornithidae Fürbringer 1888.

Gastornithiform skeletons have tended to be preserved by virtue of their large size and resistance to weathering and abrasion during fluvial transport. North American samples of *Diatryma* consist mainly of pedal phalanges and the compact ends of long bones. Substantially complete skeletons, such as the specimen of *D. gigantea* depicted in Figure 2, are exceedingly rare. Depositional environments and associated floras and faunas indicate that the Diatrymidae inhabited coastal lowlands and alluvial floodplains. Although eurytopic, diatrymids may have preferred humid, well-vegetated backswamps that were doomed to contract once the period of relative tropicality of the early Tertiary came to a close. Their presumed close relatives, the screamers (Anhimidae), survive as relicts in comparable habitats in the Neotropics.

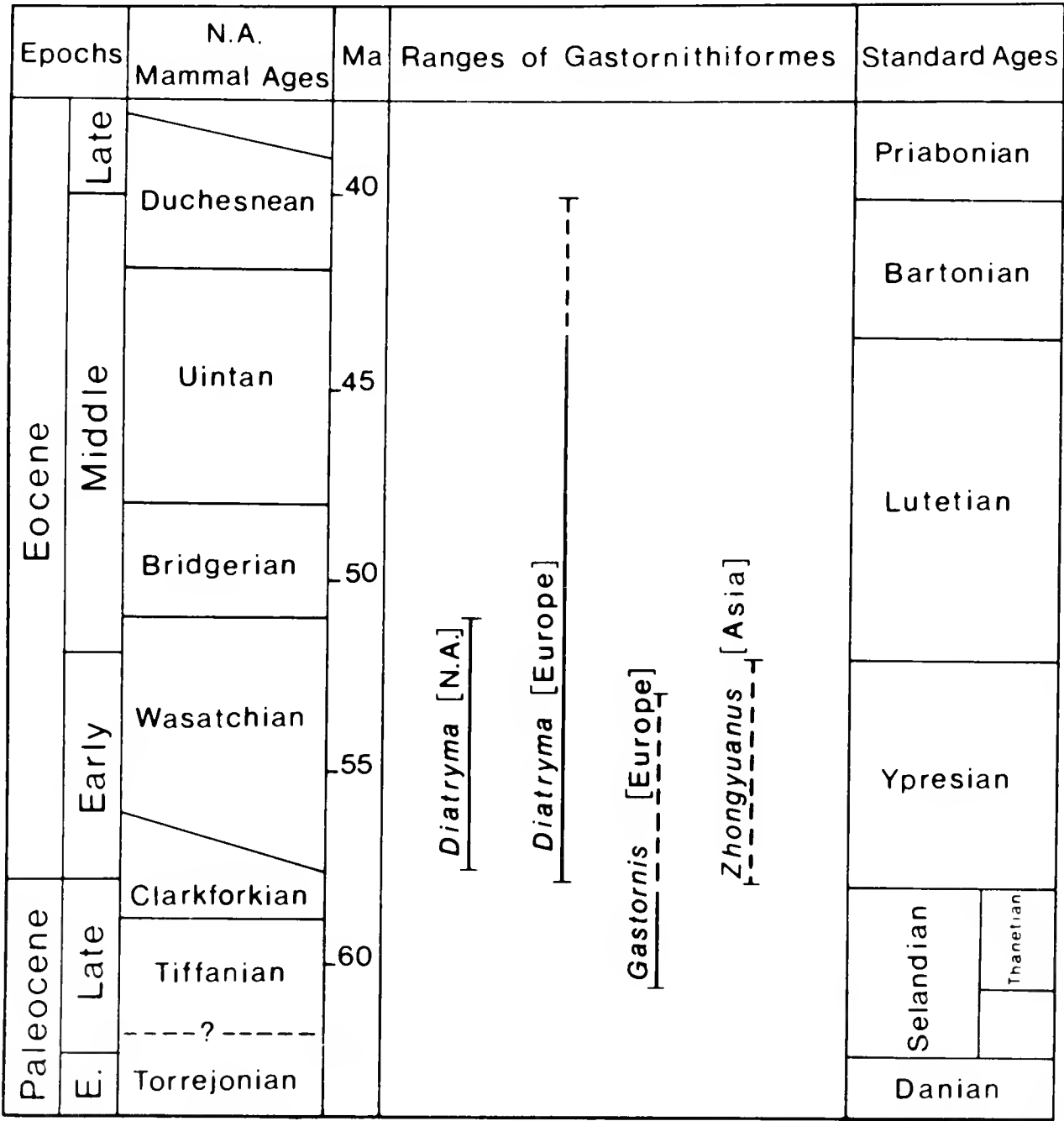


FIGURE 1 - Geochronologic ranges of the genera of Gastornithiformes. Source: Andors (1988).

Two European (*Diatryma sarasini* Schaub, *D. geiselensis* Fischer) and two predominantly North American [*D. gigantea* Cope, *D. regens* (Marsh)] species of *Diatryma* are currently recognized (Andors 1988). *D. gigantea* may have ranged across a North Atlantic land bridge into Europe (Berg 1965, McKenna 1975, Andors 1988). *D. cotei* Gaillard from France has been removed from the Diatrymidae and placed with Aves Incertae Sedis (Andors 1988). The European diatrymids and the four Eurasian species of Gastornithidae (*Gastornis parisiensis* Hébert, *G. edwardsii* Lemoine, *G. klaasseni* Newton, *Zhongyuanus xichuanensis* Hou) are in need of revision.

In a review of the North American Diatrymidae, I suggested that some traditional notions concerning *Diatryma* may be incorrect (Andors 1988). In this report I start with an overview of gastornithiform anatomy, then focus on the phylogeny and paleobiology of *Diatryma* as the first part of a projected revision of the Gastornithiformes.

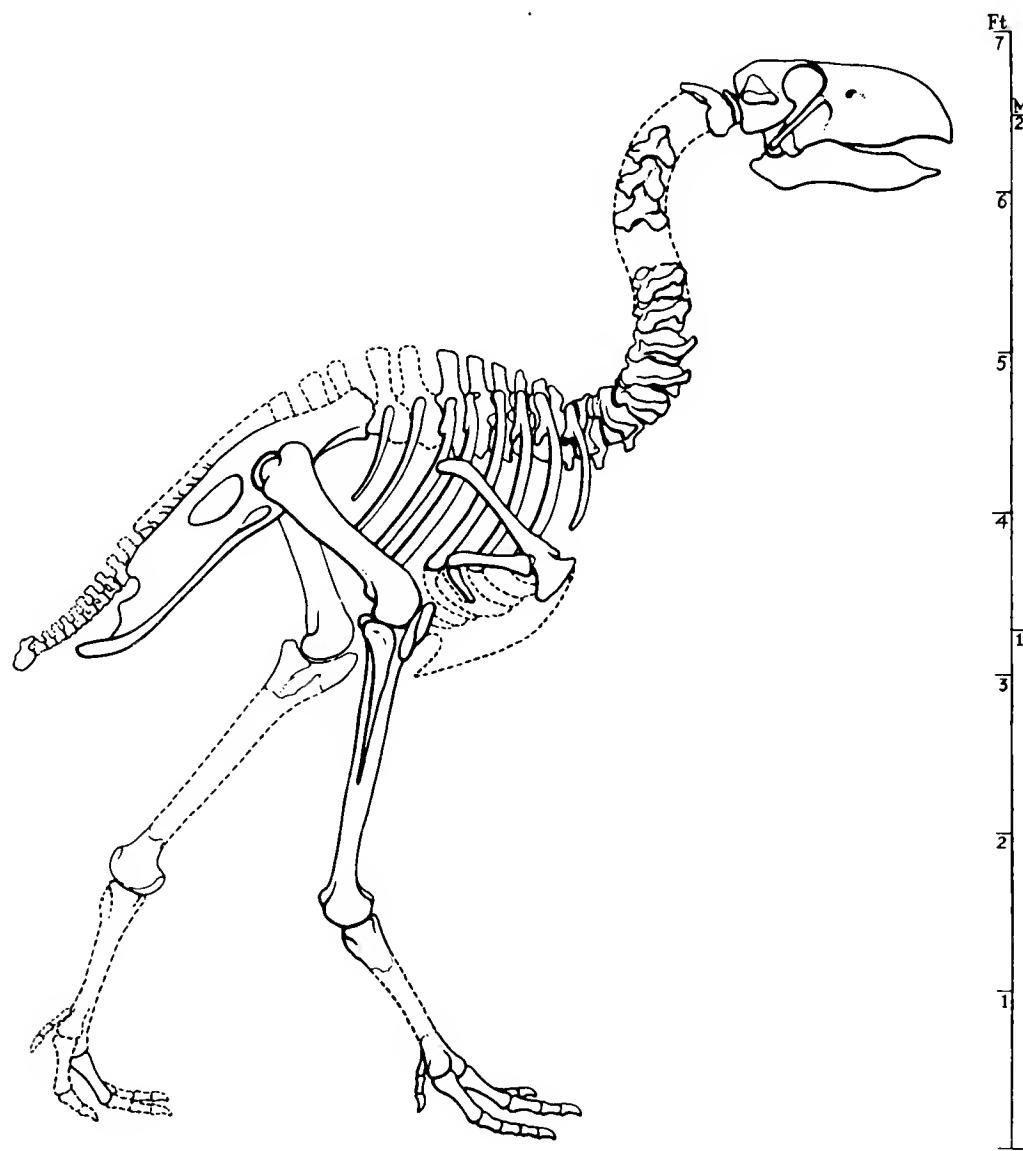


FIGURE 2 - Reconstructed skeleton of *Diatryma gigantea*, after Matthew & Granger (1917).

GENERAL FEATURES OF *DIATRYMA*

The general features of *Diatryma* are set forth in Matthew & Granger (1917), Fischer (1978), and Andors (1988, which should be consulted for a description of the diatrymid skeleton and a diagnosis of the Diatrymidae). Knowledge of diatrymid osteology is based mainly on the type of *Diatryma steini* Matthew & Granger (= *D. gigantea* Cope) (Figure 2). Adults of this species stood about 2 m tall and weighed roughly 175 kg (Andors, 1988).

The skull of *Diatryma* was huge, measuring about 45 cm in length, of which the greater part (29 cm) was taken up by the powerful, laterally compressed rostrum. The premaxilla was only slightly decurved, not hooked as in raptorial birds. The neck was very thick, measuring almost 18 cm across the posteriormost cervical. The dorsal vertebrae bore stout neural spines and were separate, not ankylosed to form a notarium. The synsacrum was short anteriorly and had an elongate caudal region. The caudals were typically amphicoelous, and the terminal 3 or 4 segments were fused to form an ovate or triangular pygostyle. The ribs lacked uncinat processes. The coracoid and scapula were fused at an angle approaching 180°. The wing was vestigial. The length ratio for the humerus, ulna, and carpometacarpus was approximately 2.6:1.3:1, indicating that the antebrachium and manus were reduced. The humerus was pachyostotic, and this and the other long bones of the wing had reduced articular surfaces. The pelvis was wide and long posteriorly, with extensive fusion between the ilium and ischium. The pelvic limbs were stout and moa-like in size and proportions, with a length ratio for the femur, tibiotarsus, and tarsometatarsus of approximately 0.75:2:1. The feet were tetradactyl and anisodactyl, with a phalangeal formula of 2-3-4-5 for pedal digits I-II-III-IV. Digits I, II, and IV were respectively 35, 71, and 81% as long as digit III, which was the stoutest of the toes. Digit I was reduced but retained some function in locomotion and prehension, extending to the ground. Digits II-IV were dorsoventrally flattened and intermediate in degree of reduction of distal segments between cursorial ostriches (*Struthio*), with more reduced toes, and pedestrian bustards (*Ardeotis*), with less reduced digits. The terminal phalanges lacked prominent flexor tubercles.

RELATIONSHIP TO GASTORNITHIDAE

The close relationship between *Diatryma* and *Gastornis* suspected by Cope (1876) has been verified by restudy of the type of *G. edwardsii* (Martin 1983) and by analysis of pelvic limb characters in *Diatryma*, *Gastornis*, and *Zhongyuanus* (Andors 1988). According to Martin (1983: 323), "There seems to be no adequate evidence to keep the Diatrymidae separate from the Gastornithidae, although the genera *Diatryma* and *Gastornis* should be kept as separate on the basis of details of the tarsometatarsus." The type and only known specimen of *Zhongyuanus xichuanensis*, a distal tibiotarsus, is distinguishable from *Gastornis* and *Diatryma* on the basis of its larger size, relatively larger lateral condyle, and somewhat more obliquely oriented supratendinal bridge (Andors 1988). Inclusion of this taxon in the Gastornithidae (Hou 1980) should be regarded as provisional in the absence of more complete material.

BROADER AFFINITIES

Diatryma has been considered to be related to the Palaeognathae (Cope 1876), Psittaciformes (Andrews 1917), Ciconiiformes (Troxell 1931), Gruiformes (Matthew & Granger 1917, Brodkorb 1967, Fischer 1978), and Anseriformes (Shufeldt 1909, Andors 1988). Only the ratite and gruiform hypotheses of diatrymid affinity have ever received wide currency. Matthew & Granger (1917) showed that the massive head and neck, neognathous palate, and extensively fused ilium and ischium of *Diatryma* precluded a near relationship to palaeognaths. Andors (1988) found that the features used by Matthew & Granger (1917) to ally *Diatryma* with gruiforms were superficial

TABLE 1 - Postulated synapomorphies for the Galloanserae (Galliformes s.l. + Gastornithiformes + Anseriformes) and Anserimorphae (Gastornithiformes + Anseriformes). For further details, see Andors (1988).

GALLOANSERAE

1. Otic process of quadrate with narrow or obsolete incisure, forming a more or less unitary joint ball.
2. Process for origin of m. adductor mandibulae externus caudalis present on otic process of quadrate.
3. Mandibular condyles of quadrate two in number, separated by a shallow intercondylar sulcus and forming a bilobate configuration in which the lateral condyle is larger and more bulbous than the medial condyle.
4. Articular fossa of mandible bipartite, inclined posteriorly, with the axes of the lateral cotyla, crista intercotylaris, and medial cotyla mutually parallel and directed anteromedially.
5. Lateral mandibular process rounded and prominent laterally, projecting abruptly from the ramal axis and forming approximately a right angle with the retroarticular process.
6. Retroarticular processes long, upwardly curved, bladelike, and laterally compressed.

ANSERIMORPHAE

7. External nares restricted to a posterior position.
8. Labial process of premaxilla very deep.
9. Nasal-frontal hinge a distinct, transverse crease.
10. Head of lacrimal moderately developed, situated beneath nasal-frontal hinge.
11. Descending process of lacrimal variable in length and width, but typically short, broadened and forked distally, projecting freely into antorbital vacuity without bracing or approximating the jugal bar.
12. Bony palate desmognathous.
13. Basipterygoid (parasphenoid) articulation of pterygoid medial in position, forming a prominent, longitudinally extensive flange.
14. Medial mandibular condyle of quadrate compressed anteroposteriorly and elongated in an anteromedial direction.
15. Medial mandibular process of mandible expanded distally and flattened or faceted anteriorly or anterodorsally.
16. Coracoid relatively short, broad-based.
17. Sterno-coracoidal process very prominent, truncated squarely at tip.
18. Minor metacarpal (IV) almost straight and oriented parallel to the major metacarpal (III).
19. Renal fossa of pelvis shallow.
20. Caudal iliac crest moderately developed or obsolete.
21. Iliac recess moderately developed or absent.
22. Femoral condyles markedly divergent posteriorly.
23. Medial condyle of tibiotarsus with extreme anteroposterior elongation and strong medial inflection.
24. Intercondylar incisure of tibiotarsus very wide.
25. Intercondylar prominence of tarsometatarsus broad, bulbous.
26. Hypotarsus typically oblong.
27. Inner condyle of trochlea metatarsi IV produced anteriorly.

(pelvic structure), derivationist (supposed derivation of the diatrymid otic process and pelvis from *Cariama*-like stages), possibly convergent (desmognathous palate), or hypothetical (supposed narrowness of the sternum). He also found that the *Diatryma*-like features reported in the skulls of parrots (Andrews 1917) were attributable to convergent evolution of herbivory, and that the interpretation of *Diatryma* as a "colossal heron" (Troxell 1931) was contradicted by cranial evidence. Shufeldt's (1909) placement of *Diatryma* in the Anseres (= Anseriformes auct.) was an American extension of a European tradition of placing *Gastornis* and its allies in the neighborhood of waterfowl that began with Hébert (1855a,b). No supporting evidence for the assignment was given by Shufeldt. The anseriform affinities of *Diatryma* were not verified until Andors (1988) showed that Shufeldt's intuition was essentially correct.

The first cladistic analysis of diatrymid relationships (Andors 1988) showed that the Gastornithiformes (represented by *Diatryma*) is a sister-group of the Anseriformes, and demonstrated a possible sister-group relationship between the Galliformes and *Diatryma* + Anseriformes (Table 1).

Galliformes, *Diatryma*, and Anseriformes share several features of the quadrate (1-3) and articular (4-6) that are presumed to be synapomorphic. *Diatryma* and Anseriformes (Anhimidae + Anseranatidae + Anatidae), in turn, possess several features of the rostrum (7-8), craniofacial hinge (9), lacrimal (10-11), bony palate (12-13), quadrate (14), mandible (15), pectoral girdle (16-17), wing (18), pelvis (19-21), and pelvic limb (22-27) that I would interpret as shared-derived characters. The resemblances between *Diatryma* and Anseriformes are pervasive but subtle and are partly masked by gigantism and trophic specialization in *Diatryma*. In retrospect, it seems no more surprising that flightless giants with the specialized habits of gastornithiforms should comprise a sister-group of the Anseriformes, including screamers (Anhimidae), than that screamers, with their fowl-like bills and herbivorous diet, should prove to be the sister-group of the trophically varied ducks, geese, and swans (Anseranatidae + Anatidae), a relationship recognized long ago by Parker (1863).

The large size, highly derived feeding apparatus, and reduced wing of *Diatryma* justify recognition of the Gastornithiformes as a separate order. From the dual alliance with galliforms and anseriforms proposed above, there is justification for placing the Gastornithiformes with the Anseriformes in the Anserimorphae of Sibley et al. (1988), and for placing the latter and Galliformes (Gallomorphae) in the superorder Galloanserae as advocated by Sibley.

The oldest known anseriform (*Presbyornis*), the oldest known gastornithiform (*Gastornis*), and the oldest known galliform (*Gallinuloides*) are all found in the Paleogene of the Northern Hemisphere. If *Diatryma* has been allied correctly with anseriforms and galliforms, then its zoogeographic affinities may lie with Laurasia and, perhaps, Euramerica.

FEEDING ADAPTATIONS AND PALEOECOLOGY

Carnivory, herbivory, and necrophagy have alternately been suggested as modes of feeding for *Diatryma*, and it has also been hypothesized that the Diatrymidae (and the analogous Phorusrhacidae) invaded the bipedal carnivore niche left vacant by the

extinction of dinosaurs in the Late Cretaceous (Gould 1986). The first functional analysis of the diatrymid jaw apparatus (Andors 1988) showed that *Diatryma* may have been herbivorous (see also Watson 1976) and that the popular conception of diatrymids as cursorial predators is unfounded.

The skull of *Diatryma* was prokinetic and coupled movements of the upper and lower jaws appear to have been possible. Tomial morphology and outward form of the rostrum and mandible indicate that the jaws of *Diatryma* constituted a formidable slicing and crushing mechanism. The considerable breadth of occiput and thickness of neck imply that the jaw apparatus of this bird was deployed against considerable resistance.

Several features of the jaws of diatrymids are shared with Recent avian folivores and can be interpreted as indications of folivorous habits in *Diatryma*. These include: a high, laterally compressed, heavily ossified rostrum with a steeply arched culmen; stout labial processes of the premaxillae; stout lateral nasal bars; restricted nares; a well-developed nasal-frontal hinge; condylar jugal-maxillary articulations; a massive mandible with an elongate symphysis and deep rami; and rostral and mandibular tomia differentiated into a seizing/cropping region in front and a slicing/crushing region behind. The closest modern analogues to the feeding mechanism of *Diatryma* are found in the Takahe *Porphyrio mantelli* (Rallidae), Kakapo *Strigops habroptilus* (Psittacidae), and Hoatzin *Opisthocomus hoazin* (Opisthocomidae), which are folivores that either fly poorly (*Opisthocomus*) or are flightless (*Porphyrio*, *Strigops*). Not coincidentally, the Kakapo and Takahe are respectively the largest living parrot and rail.

Large body size in *Porphyrio*, *Strigops*, and *Diatryma* is evolutionarily related to flightlessness and folivory (Morton 1978; Andors 1988). Leaves require a long retention time for the extraction of energy, and they must be eaten in bulk and accommodated by a large storage space in the alimentary canal in order to be utilized efficiently. The added weight, long retention time, and slow energy release of a diet of leaves are disadvantageous to a flying animal. Birds that subsist on leaves have accordingly tended to forfeit the energetic expense of flight and evolved large size. An exception is *Opisthocomus*, a volant, 750-g bird that has been able to remain small and to retain flight capability by evolving ruminant-like foregut fermentation (Grajal et al. 1989).

The folivorous niche apparently occupied by *Diatryma* is without parallel in modern landscapes, which do not possess birds of precisely the same ecology and imposing size. Although several unrelated birds have convergently evolved *Diatryma*-like features related to diet, none have duplicated the strange amalgam of parrot-like and rail-like characters that attest to the browsing or grazing habits of this extinct anseriform relative.

LOCOMOTORY ADAPTATIONS

The forelimb of *Diatryma* has been reduced to about the same proportion of the leg as the wing of kiwis (*Apteryx*), emus (*Dromaius*), and extinct flightless geese (*Thambetochen*) (Andors 1988). The rudimentary wing of *Diatryma* is comparable in

predigital length (31 cm) to the relatively larger wing of a flying bird weighing a few kg or less. From the disproportion between the diatrymid wing and body, it is apparent that the wing has diminished in relative length while body size has increased. Transformation series of dinosaurian and avian forelimbs indicate that forelimb reduction in obligate bipeds, including *Diatryma*, has tended to be concentrated distally (Andors 1988).

The principal locomotory adaptations of *Diatryma* reside in the leg, which resembled the hind limb of kiwis (*Apteryx*), anomalopterygine moas (*Anomalopteryx*, *Pachyornis*), elephant-birds (*Mullerornis*, *Aepyornis*), and dodos (*Raphus*) in intramembral proportions (Andors 1988). It appears unlikely that *Diatryma*, moas, and elephant-birds, with their stout builds, wide pelvises, and relatively short tarsi, could have run as rapidly as ostriches (*Struthio*; maximum speed 12-17 m/s), in which the postacetabular pelvis has been narrowed and the tarsometatarsus lengthened. In *Diatryma*, the massive, elongate femur (relatively longer than in any ratite except *Apteryx*), short tarsometatarsus, and rather short, heavy toes may imply graviportal posture and locomotion, which have been inferred for other large flightless herbivores, including moas, elephant-birds, and dodos. The intramembral proportions of the anterior toes (II-IV) of *Diatryma* are bustard-like, but the retention of a functional hind toe (I) distinguishes diatrymids from more cursorially adapted groundbirds, including ostriches (*Struthio*), rheas (*Rhea*), cassowaries (*Casuarius*), emus (*Dromaius*), and bustards (*Otididae*), in which the hallux has been lost. The unguals of toes II-IV are somewhat hooflike and destitute of prominent flexor tubercles, indicating that the foot of *Diatryma* was better suited for pedestrian ground activity than for perching or for grasping prey.

It thus appears likely that *Diatryma* had a slow gait, like bustards, and a bustard-like aversion to rapid running (Andors 1988). This conclusion is at variance with the traditional conception of gastornithiforms as running birds (e.g. Simpson 1950).

CONCLUSION

The phylogenetic affinities of the Gastornithiformes have long been misinterpreted, owing mainly to the efficacy of gigantism in masking phylogenetically significant features in the skeleton. Restudy of *Diatryma* discloses that the Gastornithiformes are the sister-group of the Anseriformes, and that the Galliformes may be the sister group of the Gastornithiformes + Anseriformes. All three orders may have originated in the Northern Hemisphere.

Diatrymids were pedestrian herbivores, not cursorial predators as usually assumed. The skull of *Diatryma* was prokinetic and apparently primarily adapted for folivory. The wing of this ponderous bird was reduced distally in concert with evolutionary increase in body size. The pelvic limb was apparently best suited for walking, not running. Though it may have competed with other herbivores for resources or fed opportunistically on small game or on carrion, *Diatryma* was mainly herbivorous, to judge from its skull morphology, large size, flightlessness, anseriform affinities, and environmental preferences. Its general aspect and habits were similar to those of the living Takahe of New Zealand, which evolved the resemblances convergently and in isolation.

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ZOOGEOGRAPHICAL RELATIONSHIPS OF THE EOCENE AVIFAUNA FROM MESSEL (GERMANY)

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ABSTRACT. The fossil avifauna from Messel (Lower Middle Eocene) comprises at present 20 families, which can be divided into three groups: (1) More than half of the families have no contemporary or older members outside Europe. Some of them reached North America later on, apparently via a North Pacific connection. (2) Six families have contemporary or older members in North America. They could have used a North Atlantic connection. (3) Palaeotididae and Phorushacidae have their closest relatives in South America. This distribution pattern is parallel to that of several other groups of animals. It is best explained by the hypothesis that these animals entered Europe via a temporarily existing trans-Tethys connection between Africa and Europe. This hypothesis permits one to predict that the two families should exist also in Africa, provided that the appropriate fossil deposits are available.

Keywords: Zoogeography, Messel avifauna, fossil birds, avian relationships, evolution, Eocene.

INTRODUCTION

Zoogeographical work on the rich Eocene fauna from Messel (Lower Geiseltalian) has concentrated largely on mammals (Koenigswald 1981, Storch 1984, 1986, Storch & Schaarschmidt 1988). Birds were treated only briefly (Peters 1988, Storch & Schaarschmidt 1988). At least 20 bird families are represented among the fossils from Messel. Other, as yet unidentified families might be present in the scattered collections from this site. In this paper I review the avian taxa that have been identified to date in the Messel avifauna. This analysis is done using the systematic sequence starting with Struthioniformes and ending with Passeriformes. Extinct families are indicated by a dagger (†). For each family rank taxon a description is given to emphasize especially significant features (anatomical and distributional). Preliminary zoogeographical conclusions are drawn from the evidence reviewed in this report.

THE EOCENE MESSEL AVIFAUNA

Struthioniformes

1. †Palaeotididae Houde & Haubold. The only species, *Palaeotis weigelti* Lambrecht, displays a distinctive combination of osteological features. Its palate is similar to the conditions in the Lithornithiformes and Tinamiformes, whereas many postcranial elements are close to the conditions in the Rheidae (Peters 1988). *Palaeotis* is known from the Geiseltal and Messel. The earliest relatives of the rheas are known from the Paleocene of Brazil (*Diogenornis fragilis* Alvarenga). Other ratites have been recovered in France (Paleocene), Switzerland (Eocene), England and Egypt (Oligocene), Moldavia, Argentina, and Australia (Miocene), Greece, the Ukraine, Kazakhstan, India, China, Mongolia, Argentina, and Australia (Pliocene).

Accipitriformes

2. Accipitridae Vigors. The single small species known from Messel is the earliest record for this family (description in press). Other Eocene, but younger, records came from England and France. Still younger records are widespread, especially on northern continents. Accipitrids occur world-wide today.
3. Falconidae Leach. A juvenile specimen from Messel was tentatively assigned to the subfamily Polyborinae (Peters 1989). Very few species have been described from the Tertiary. The earliest are *Parvulivenator watteli* Harrison and *Stintonornis mitchelli* Harrison from the Lower Eocene of England. However, I am not convinced that the identification of *Parvulivenator* is correct. Other Tertiary falconids are reported from France, Argentina, Nebraska, and Kazakhstan. The family has a world-wide distribution today with greatest taxonomic diversity in South America.

Galliformes

4. Family indet. There is at least one galliform species among the Messel birds. Other Eocene species are known from England, France, and Wyoming. They were assigned to the Megapodidae, Gallinuloididae, Cracidae, and Phasianidae, respectively. A revision of the differential diagnoses is desirable.

Ordo incertae sedis

5. Plataleidae Bonaparte. *Rhynchaetites messelensis* Wittich, a small ibis, was the first avian species described from Messel (Peters 1983). There is a somewhat doubtful species from the Lower Eocene of England. Younger Tertiary ibises come from France, England, China, North America, and Argentina. Since the Plataleidae are a comparatively old group (Olson 1979, Peters 1983), one should expect fossil ibises from much earlier deposits.

Gruiformes

6. †Diatrymidae Shufeldt. The only record from Messel is an imprint of a single femur (Berg 1965). The species seems to be identical with *Diatryma geiselensis* Fischer known from the Geiseltal. The Diatrymidae were distributed in North America and Europe during the Eocene. The systematic status of the family is controversial. *Diatryma* may not even belong to the Gruiformes. Andors (1988) revised *Diatryma* and determined that it and the related Gastornithidae comprise a sister-group of the Anseriformes.
7. †Phorushacidae Ameghino. Most species of this family of large flightless birds have been recovered in South America (Oligocene to late Pliocene), but one species is known from the late Pliocene of Florida. *Ameghinornis minor* (Gaillard) was discovered in the Eo-Oligocene Phosphorites of Quercy (France). The earliest species so far is *Aenigmavis sapea* from Messel (Peters 1987).
8. Cariamidae Bonaparte. At least three undescribed species of this family are among the Messel birds. They precede temporally the numerous species from France (Upper Eocene, Oligocene) and North America (Upper Eocene - Lower Miocene). The family is now restricted to two species in South America.
9. †Messelornithidae Hesse. *Messelornis cristata* Hesse is by far the most common avian species from the Messel pit. Several other species of this family are known from the Eocene and Oligocene of France and North America. The closest extant

relatives of the family are the sunbitterns (Eurypygidae) represented by a single species in South America (Hesse 1989). No fossil sunbitterns are known.

Charadriiformes

10. Phoenicopteridae Bonaparte. The type specimen of *Juncitarsus merkei* Peters from Messel provided important arguments supporting the view that flamingos are charadriiform birds (Olson & Feduccia 1980). The genus *Juncitarsus* Olson & Feduccia is represented also in the Eocene of North America. Late Tertiary fossil flamingos were widely distributed, with a range that included Australia.

Strigiformes

11. †Palaeoglaucidae Mourer-Chauviré. A single species is known from Messel (description in press). Another species was described from Quercy, France (Mourer-Chauviré 1987). The Palaeoglaucidae display a mixture of osteological features that have been alternately attributed to the Tytonidae or the Strigidae. Numerous owls, definitely different from the Palaeoglaucidae, have been recovered from the Tertiary of Europe and North America. At present owls are cosmopolitan in distribution.

Caprimulgiformes

12. Podargidae Bonaparte. This family is represented by a single undescribed species. Mourer-Chauviré (1989) described another species from the Upper Eocene of Quercy, France. No other fossil records exist. Today the Podargidae are confined to Australasia.
13. Caprimulgidae Vigors. A single species was recovered in the Messel pit. Again the only other named fossil species, *Ventivorus ragei* Mourer-Chauviré, comes from Quercy. However, at least one more species from the Green River Formation, Wyoming, seems to exist (Grande 1980: Figure III.20). At present nightjars are found on all continents, except in the coldest regions.

Apodiformes

14. †Aegialornithidae Lydekker. This family is confined to the Eocene of Europe. The oil shale of Messel produced the smallest species, *Aegialornis szarskii* (Peters 1985). The earliest species comes from the Lower Eocene of England (Harrison & Walker 1975). Other species are known from France (Mourer-Chauviré 1988).

Ordo indet., incertae sedis

15. †Family unnamed. This enigmatic group is represented by two fairly complete skeletons from Messel. Their size is that of a European Starling. Their feet are pamprodactyl, with extremely shortened toes and rather strong claws, thus reminding one of swifts. However, the tarsometatarsus is slender and much longer than the longest toe. The proportions give the impression of a faulty "nonfunctional" construction. The remainder of the skeleton is not swift-like at all. Unfortunately most bones are badly crushed and deformed. One of the specimens had the crop or the stomach filled with seeds.

Piciformes

16. †Family indet. Several specimens from Messel represent different species. They are assigned to the Piciformes for convenience. Although similar in some respects to the Capitonidae they seem to belong to a separate family. The fossil record of

the Piciformes is poor. Several species supposed to belong to this order are now assigned to the Coraciiformes (Olson 1985). Indicatoridae are known from the Lower Pliocene of South Africa. The earliest barbets and woodpeckers have been recovered from Miocene deposits of Europe and North America.

Coraciiformes

17. Coraciidae Rafinesque. Among the Messel birds this family is represented by at least two or three unnamed species. The only other fossil records come from Quercy (Mourer-Chauviré 1989) and North America (Olson 1985).
18. †Family unnamed. This group includes fossil birds with an overall coraciiform appearance but with raptorial feet. At least two species are known from Messel. They seem to be very close to *Eobucco* Feduccia & Martin. Other species come from the Eocene of North America.
19. †Sylphornithidae Mourer-Chauviré. These tiny birds are known so far only from the Upper Eocene of Quercy (Mourer-Chauviré 1988). At least one species, however, lived also in the forests around the Eocene lake of Messel. Its size was about that of the hummingbird *Chrysolampis mosquitus*.

Ordo?

20. cf. †Primoscenidae Harrison & Walker. This family was established on the basis of a single fragmentary carpometacarpus from the London Clay. The characteristic configuration of this carpometacarpus was observed again in a small bird from Messel. This specimen is a complete skeleton similar in size and superficial appearance to a today. Closer examination revealed a mixture of features that are found in todies, ground-rollers, and passerines. There are probably more specimens from Messel belonging to the same group. Whether these birds are to be regarded as coraciiform or passeriform is unclear. Passerines do not appear in the Northern Hemisphere until the late Oligocene.

DISCUSSION AND CONCLUSIONS

The information summarized above suggests that the zoogeographical relationships of taxa from Messel have changed with time. There are at least two possible explanations of this result. The first is that the ranges of species *did* change, and that the fossil record mirrors these changes.

The second explanation emphasizes the incompleteness of the fossil record. The fossil records of North America and Europe are probably better known than those of other areas. Thus, the lack of a certain taxon in North America or Europe has a stronger bearing on zoogeographic questions than a similar lack elsewhere (e.g. Africa or South America). Bearing these points in mind, the data at hand enable one to distinguish three categories of zoogeographic relationship.

1. A number of families from Messel have no contemporary or older members outside Europe (families 2,3,5,8,11,12,14-16,19,20). I omit the unnamed piciform family whose phylogenetic relationships are unclear. Among the remaining 10 families, the Aegialornithidae, the Sylphornithidae, the Primoscenidae and the enigmatic family 15 seem to be confined to the Eocene of Europe. The same may

be true of the Palaeoglaucidae, unless they represent the ancestors of the Strigidae.

The record of the Podargidae shows a large gap between the Eocene and the Recent. The Podargidae presumably vanished from Europe at the end of the Eocene. One should expect to find fossil frogmouths in the southern regions of the Old World.

The remaining four species are found in younger deposits of the Tertiary of North America. If this reflects the actual timing of dispersal events, then these birds could have reached America by a North Pacific connection, since the North Atlantic connection was interrupted in the Early Eocene (Briggs 1987). The Cariamidae might have reached their present range in South America via North America. Their earliest South American record is from the late Pliocene (Tonni 1974). Dispersal across the North Pacific connection implies that fossils from these families should be expected in Asian deposits.

2. Six families represented at Messel have contemporary (9,10,13,17,18) or older (6) members in North American deposits. For these birds an exchange between Europe and America was possible via the North Atlantic connection. The galliform family (4) may have to be included in this group. However, it is omitted here because its systematic position is unclear.
3. The fossil records of the Palaeotididae and the Phorusrhacidae raise interesting zoogeographical questions. The European species of both families have their closest relatives in South America. Phorusrhacidae are known also from the late Pliocene of Florida. Phorusrhacids may have entered North America after the emergence of a Central American connection (Brodkorb 1963; Olson 1985; Vuilleumier 1985).

The data at hand suggest three possible explanations: a) The appearance of close relationship between the European and South American birds may in fact be due to convergence. b) Phorusrhacidae and rhea-like ratites inhabited North America also; their fossils have not been recovered yet. c) Both families evolved on the southern supercontinent prior to the complete separation of South America and Africa. The birds invaded Europe from Africa.

The third alternative is a daring hypothesis. Nevertheless I prefer it because it is supported by several parallel cases from other groups of animals, notably mammals (Storch 1981, Gheerbrant 1987, Storch & Schaarschmidt 1988). There existed, apparently, a trans-Tethys connection in the late Mesozoic-early Cenozoic that permitted faunal exchange between Africa and Europe. If this hypothesis is correct, corroborating fossil remains should be expected from African Cretaceous and Tertiary deposits.

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RECONSTRUCTING THE HISTORY OF *NOTHOFAGUS* FOREST AVIFAUNAS

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ABSTRACT. Forests with southern beeches (*Nothofagus*, Fagaceae) occur disjunctly in South America, Australia, Tasmania, New Zealand, New Guinea, New Britain, and New Caledonia. The Recent and fossil distribution of *Nothofagus* point to a Gondwanan evolution. Do birds of *Nothofagus* forests show a parallel history? *Nothofagus* avifaunas consist of 323 species. Species diversity is highest in New Guinea (140 species), but is much lower elsewhere (28-42 species). Quaternary sites in New Zealand have fossil birds that lived in *Nothofagus* forests, but no Tertiary avian fossils are associated with *Nothofagus*. Only indirect evidence from Recent taxa is available to reconstruct the history of *Nothofagus* forest birds. Some taxa (old autochthons) have had a long history in or near their present geographic location. Other taxa are derived autochthons, whereas still others are more recent arrivals in *Nothofagus* forests (self-introduced, or man-introduced). Older taxa are confined to one side of the Pacific basin or the other. More recent ones are derived from nearby areas. Thus there is little evidence for a Gondwanan history of *Nothofagus*-associated birds.

Keywords: *Nothofagus*, biogeography, avifaunas, evolution, South America, SW Pacific, Gondwana.

INTRODUCTION

Southern beeches of the genus *Nothofagus* are perhaps the quintessential "Gondwanan taxon" in Southern Hemisphere biogeography. Many workers have discussed their distribution and the history of their present disjunction (e.g. Cracraft 1975, Cranwell 1963, Darlington 1965, Heads 1989, Humphries 1981, Lovis 1989, Romero 1986, van Steenis 1971). Other plant taxa (Skottsberg 1960), several arthropod taxa (e.g. Hennig 1960, Brundin 1966), and some vertebrate taxa (e.g. galaxiid fishes: McDowall 1990, McDowall & Whitaker 1975) also exhibit Gondwanan patterns.

Traditionally, the bird faunas of the southern tips of the southern continents and New Zealand have been placed in different faunal groups corresponding to Sclater's faunal regions. However, Cracraft (1973) suggested that 17 families found in South America, 11 in Australia, and 3 in New Zealand belonged to trans-Antarctic "Southern Hemisphere Dispersal Groups". Later, Cracraft (1975) listed several pairs of vicariant sister-taxa between South America and Australia and between South America and New Zealand, but in his analysis of *Nothofagus* biogeography, he did not mention any bird group that might be linked biogeographically to *Nothofagus*.

In this report we present a preliminary analysis of the avifaunas associated ecologically with *Nothofagus* forests of the world, and review by way of selected examples the relationships that might permit reconstruction of these faunas. This exercise has not been attempted previously, except for a discussion of niches occupied by *Nothofagus* forest birds (Kikkawa 1974, 1984) and an attempt at reconstructing the history of South American *Nothofagus* avifaunas (Vuilleumier 1985).

MATERIAL AND METHODS

We have carried out field and museum studies of *Nothofagus* birds as follows: J.K. in New Zealand (1958-1960), Tasmania (1962), New South Wales (1961-1964), Queensland (1965-1970), New Guinea (1969,1970), and South America (1971); F.V. in South America (1965,1985,1987 [2 trips], 1988), New Zealand (1974,1990), New Caledonia (1974,1978), mainland Australia (1974,1989,1990), Tasmania (1989), New Guinea (1989), and New Britain (1990). Our earlier work has resulted in several publications (Kikkawa 1966,1968,1974,1984, Kikkawa et al. 1965, Vuilleumier 1967a,b, 1972, 1985). Museum work was done especially at the American Museum of Natural History. F.V. also carried out field work in *Fagus* forests of central Europe and temperate rainforests of SE Alaska, regions used as north-temperate "controls." F.V. has field experience with about 210 of 323 species and about 150 of 193 genera.

We made a list of *Nothofagus* forest birds on the basis of our field work and a literature review, using the sequence and nomenclature of Morony et al. (1975). We then analyzed distributional and systematic relationships among these birds. Extinct avian taxa listed in the text are indicated by a dagger (†).

DISTRIBUTION OF *NOTHOFAGUS*

The genus *Nothofagus* (Fagaceae) has about 37 species: 11 in South America, 4 in New Zealand, 2 in Tasmania, 2 in Australia, 5 in New Caledonia, and about 13 in New Guinea, including the main island of New Guinea, New Britain, and two of the d'Entrecasteaux Islands, Normanby and Goodenough (Van Steenis 1972). Our own field work thus covers all areas with *Nothofagus* except Normanby and Goodenough, J.K. being more familiar with SW Pacific areas and F.V. with South America. The systematic position of species (and species groups) within the genus *Nothofagus* is far from settled, as is also the systematic position of *Nothofagus* within the Fagaceae or the Fagales, as well as the relationship between Northern Hemisphere *Fagus* and Southern Hemisphere *Nothofagus*.

At tropical latitudes (New Guinea, New Britain, d'Entrecasteaux, New Caledonia) *Nothofagus* occurs from about 200 m (New Caledonia) to 3500 m (New Guinea). The main altitudinal belt on New Guinea is about 2000-3200 m, where pure *Nothofagus* stands often occupy large areas. On the mainland of temperate Australia, *Nothofagus* is found in isolated gullies near sea level and in mountains (Victoria) or on isolated mountaintops of the Great Divide (Queensland, New South Wales). Further south (South America, New Zealand, Tasmania), *Nothofagus* occurs from the seashore up to the timberline. In South America, the genus ranges from about 33°S to 56°S, with the southernmost *Nothofagus* scrub growing on Cape Horn.

Nothofagus forests are usually closed, dripping wet rainforests, whether under tropical or temperate latitudes. Epiphytes, mosses and ferns can be abundant. Physiognomically, *Nothofagus* forests are relatively simple among rainforest types and are similar wherever they occur. Floristically, they are usually poor in higher plants and this is most exaggerated in the southernmost forests of South America.

Fossil *Nothofagus* has been found in most regions where the genus is represented today, and in Antarctica (Cranwell 1963, Van Steenis 1971,1972). Fossil *Nothofagus* has not been found in Africa or India.

NOTHOFAGUS FOREST AVIFAUNAS

About 323 species in 193 genera and 62 families occur in *Nothofagus* forests of the world. Table 1 gives numbers of species, genera, and families for each region except the d'Entrecasteaux Islands, for which bird data are lacking. New Guinea has the richest fauna (140 species, 97 genera, 34 families). All other regions have rather similar, much smaller, numbers of taxa, 28-42 species, 26-38 genera, and 19-22 families. Note that three "control" forests in the Northern Hemisphere (two beech, *Fagus*, and one boreal) also have small numbers of taxa. Species diversity has no obvious relationship to area of *Nothofagus* forest in a given region. South America has the largest area, yet few bird species. New Guinea has many more bird species than Australia, but also has a more extensive area of *Nothofagus*. New Zealand has a greater area of *Nothofagus* than Australia, but is more isolated and has fewer bird species.

TABLE 1 - Numbers of families, genera, and species in different *Nothofagus* regions of the world.

	Numbers of taxa (totals for all regions)		
	Families (62)	Genera (193)	Species (323)
<i>Nothofagus</i> regions			
New Guinea	34	97	140
New Britain	22	33	39
New Caledonia	19	26	28
New Zealand	20	30	37
Australia	20	31	42
Tasmania	19	30	31
South America	19	38	41
"Controls"			
Japan	15	20	30
Jura	16	29	36
Alaska	18	33	39

Note: Controls are two regions in the Northern Hemisphere with *Fagus* (Japan, Jura) and one with boreal forest (Tongass National Forest, SE Alaska). Sources: Uramoto (1961), Japan; Glayre & Magnenat (1984), Jura; F.V. (unpubl.), SE Alaska.

An analysis of faunal similarity (Table 2) shows that very few genera are shared between pairs of distant regions (e.g. New Guinea and South America), but many more between nearby regions (New Guinea and New Britain). The overall similarity matrix reveals that SW Pacific areas are more similar to each other than any is to South America. Genera shared between or among regions are *Accipiter* (cosmopolitan), *Columba* (widespread), *Turdus* (nearly cosmopolitan), and genera that are widespread in the South Pacific (*Chalcites*, *Pachycephala*, *Rhipidura*, *Gerygone*, *Zosterops*).

Several family-level taxa are "unique" to a given *Nothofagus* region, in other words, occur in a given region but not in others (note that this designation is not synonymous with endemic). Examples are the Paradisaeidae in New Guinea, Cuculidae and Meliphagidae in the SW Pacific, Rhinocryptidae and Picidae in South America, and

Acanthisittidae in New Zealand. These patterns show that each *Nothofagus* area around the South Pacific Ocean basin has its own faunistic mixture including unique elements, as well as others that are more widespread. Thus the South American *Nothofagus* fauna includes families found nowhere else in *Nothofagus* regions (Picidae, Furnariidae, Rhinocryptidae) and families found elsewhere (Turdidae). The Australian *Nothofagus* fauna has unique elements (Menuridae, Atrichornithidae) and others that occur elsewhere (Turdidae). Each region thus has a unique blend of faunal elements, a pattern that implies separate histories for each region, and especially for the two halves of the South Pacific basin (the American side and the Australasian one).

TABLE 2 - Faunal similarity among *Nothofagus* forest faunas (number of genera shared between pairs of faunas).

(Number of genera)	NG (96)	NB (33)	NC (26)	NZ (28)	AU (31)	TA (26)	SA (38)
NG	—	21	14	7	13	14	2 ^a
NB		-	10	2 ^b	6	7	2 ^c
NC			-	6	9	7	2 ^d
NZ				-	6	7	1 ^e
AU					-	8	1 ^f
TA						-	2 ^g
SA							

Abbreviations: NG - New Guinea, NB - New Britain, NC - New Caledonia, NZ - New Zealand, AU - Australia, TA - Tasmania, SA - South America. Genera shared:
^aNG-SA: *Accipiter*, *Turdus*.
^bNB-NZ: *Rhipidura*, *Zosterops*.
^cNB-SA: *Accipiter*, *Columba*.
^dNC-SA: *Accipiter*, *Turdus*.
^eNZ-SA: *Turdus*.
^fAU-SA: *Accipiter*.
^gTA-SA: *Accipiter*, *Turdus*.

FAUNAL ELEMENTS

Avian biogeographers have traditionally divided faunas into elements (e.g. Mayr 1946). This approach has been criticized recently by panbiogeographers and vicariance biogeographers. Because we lack cladistic analyses of the taxa found in *Nothofagus* regions, we rely for now on conventional methods of analysis. We assign taxa living in *Nothofagus* regions to five elements: (1) old autochthons (families or genera that have been in or around *Nothofagus* forests since the early Cenozoic), (2) derived autochthons (families or genera that have probably occupied *Nothofagus* forests since the mid to late Cenozoic), (3) recent self-introduced (taxa that have reached *Nothofagus* forests in the Late Pleistocene-Holocene, or even historical times), (4) man-introduced (taxa that have been released by man in a region with *Nothofagus*, and that have established themselves in *Nothofagus* forest), and (5) unknown. We give below examples of each element.

Old autochthons

- (1) *Apteryx*, Apterygidae. This group of ratites, endemic to New Zealand, has been in this area for a long time, although exactly how long a stay is a matter for debate.

- (2) *Rhynochetos*, Rhynochetidae. Although not an ecological specialist tied to *Nothofagus* forest, this New Caledonian endemic has had a long history in its native area. It appears to be related to the Neotropical and lowland rainforest-dwelling sunbittern (*Eurypyga*, Eurypygidae).
- (3) *Atrichornis*, Atrichornithidae. One species of scrubbird is restricted to mountaintop *Nothofagus* and associated vegetation in Australia.
- (4) *Pygarrhichas*, Furnariidae. This nuthatch-like furnariid, endemic to South American *Nothofagus* forest (Vuilleumier 1985), is isolated within its family, and can be expected to have lived there for a long time.
- (5) Acanthisittidae. This endemic New Zealand family has long been acknowledged to be the representative of an old stock (Sibley et al. 1982).

Derived autochthons

- (1) *Hemiphaga*, Columbidae. Endemic to New Zealand, this genus is clearly allied to other South Pacific pigeon genera, such as *Ducula*.
- (2) *Campephilus*, Picidae. Although the South American Ivory-billed Woodpecker clearly belongs in this genus, it is not closely related to other congeners, either elsewhere in South America, or in North America (Short 1970).
- (3) *Mohoua-finschia*. This endemic New Zealand group, formerly allied with the Sylviidae, is in fact related to the Pachycephalinae of the corvid assemblage, as defined by Sibley and Ahlquist (1987a).
- (4) *Melampitta*. This New Guinea genus of ground birds, convergent on Rhinocryptidae, is a bird of paradise according to Sibley and Ahlquist (1987b). If so, then given the diversity of arboreal Paradisaeidae in New Guinea forests, including *Nothofagus* forests, *Melampitta* may be a derived and ecologically specialized line.

Recent self-introduced

- (1) *Cathartes aura*. This vulture presents subspecific differentiation in the South American *Nothofagus* area, and can be hypothesized to be a recent arrival there from more tropical areas to the north, where more species of *Cathartes* occur.
- (2) *Phylloscopus trivirgatus*. This leafwarbler occurs in *Nothofagus* and other montane forests of New Guinea and New Britain. It is the southernmost member of the genus, which has its center of diversity in the Palearctic.
- (3) *Zoothera dauma*. This wide-ranging Palearctic taxon reaches *Nothofagus* forests in Australia and Tasmania, and also occurs in New Guinea. The relative ecological independence of *Z. dauma* from *Nothofagus* forests suggests recency of occupation of this habitat.
- (4) *Gerygone*. This widespread South Pacific genus is found in a wide variety of habitat, and its occurrence in *Nothofagus* forests is thus not surprising.

- (5) *Zosterops*. A recent self-introduction to New Zealand, *Zosterops* is now locally abundant in *Nothofagus* forests (Diamond & Veitch 1981).

Man-introduced

Many man-introduced taxa are found in New Zealand, and a few in Tasmanian and Australian *Nothofagus* forests. The greatest ecological impact is felt in New Zealand, where the genera *Turdus*, *Prunella*, *Fringilla*, and *Acanthis* occur commonly in some types of *Nothofagus* forests, where they may even displace native taxa. In fact, New Zealand *Nothofagus* forests otherwise contain only a dozen or so native species.

Unknown

This category includes many taxa, the origin of which, either in or outside *Nothofagus* forests is quite unclear. They are a varied lot taxonomically and ecologically, and include taxa such as *Rallina* (New Guinea), *Gallicolumba* (New Guinea), *Calyptorhynchus* (Tasmania), *Cyanoramphus* (New Zealand), *Cacomantis* (New Guinea), *Coracina* (New Caledonia), *Oreocharis* (New Guinea), and *Corvus* (Tasmania).

SOUTHERN HEMISPHERE TAXA

Cracraft (1973) listed 28 families as "groups for which reasonable arguments can be advanced for Southern Hemisphere Dispersal." Of these 28 families, only 16 have representatives in *Nothofagus* forest regions (Apterygidae*, †Dinornithidae*, Casuariidae, Columbidae*, Psittacidae*, Cuculidae, Aegothelidae, Podargidae, Megapodiidae, Furnariidae*, Rhinocryptidae*, Menuridae*, Atrichornithidae*, Tyrannidae, Acanthisittidae*, and Phytotomidae). Only 9 (marked with asterisks) of these 16 remaining families can be considered to have a biologically important component in *Nothofagus* forests. We discuss three of these families below.

Psittacidae

"The presence of peculiar groups in Australasia, for example in the Strigopinae and Nestorinae in New Zealand and the Kakatoeinae, Loriinae, and Micropsittinae in Australia..., indicates a long period of differentiation which probably began sometime in the Cretaceous" (Cracraft 1973: 508). The South American psittacids living in *Nothofagus* forests belong to an endemic genus, *Enicognathus*, and represent long-completed speciation in this area, but these birds appear related to Andean psittacids (*Pyrrhura*), not to Australasian ones. A review of Southern Hemisphere psittacids may nevertheless be worth doing.

"Menurae"-Rhinocryptidae

Feduccia and Olson (1982) argued that the Australian "Menurae" (*Menura* and *Atrichornis*) were closely related to the South American Rhinocryptidae, which have several relict taxa in *Nothofagus* forests, and suggested (p. 17) that the "Menurae" and Rhinocryptidae "could well be interpreted as remnants of a group that originally dispersed through the Southern Hemisphere, in accordance with what is now known of plate tectonics and continental drift." This would be an interesting idea, but neither morphology (Bock & Clench 1985) nor DNA-DNA hybridization (Sibley & Ahlquist 1985) support the view that "Menurae" and Rhinocryptidae are related to each other. Furthermore, the relationship of *Menura* to *Atrichornis* is not clear (Rich, personal communication).

Acanthisittidae

The DNA-DNA evidence (Sibley et al. 1982) suggests that these *Nothofagus*-associated birds, endemic to New Zealand, have no close living relatives and "may be the oldest living group of endemic New Zealand birds..." (p.127). This apparent taxonomic isolation of the Acanthisittidae does not provide evidence for a Southern Hemisphere dispersal.

FOSSIL BIRDS AND NOTHOFAGUS

The only evidence of association between fossil birds and *Nothofagus* forests is found in New Zealand, where Late Pleistocene-Holocene deposits contain the remains of about 23 species of landbirds that were living in or at the edge of *Nothofagus* forests (Worthy & Mildenhall 1989, Worthy, personal communication). The genera (†*Megalapteryx*, †*Dinornis*, *Apteryx*, *Gallirallus*, *Strigops*, *Nestor*, *Cyanoramphus*, *Eudynamys*, †*Megaegotheles*, *Acanthisitta*, *Xenicus*, *Traversia*, †*Pachyplichas*, *Mohoua*, *Gerygone*, *Rhipidura*, *Petroica*, *Anthornis*, *Prothemadera*, and *Callaeas*) indicate a modern fauna. While these records are interesting, they do not provide us with clues about the early history of avian faunas in *Nothofagus* forest regions.

DISCUSSION AND CONCLUSIONS

Little can be said about the composition of early *Nothofagus* avifaunas. Basically, E. Pacific faunas (South American) are taxonomically distinct from W. Pacific ones (Australasian), thus suggesting an early differentiation in geographical isolation.

The possibility of trans-Antarctic (Gondwanan) relationships, as suggested through the apparent "Menurae"-Rhinocryptidae relationship, is in fact non-existent. Data on other groups, such as Psittacidae or Acanthisittidae, provide no clues. Thus for the present we conclude that *Nothofagus*-associated avifaunas are idiosyncratic and unique in their composition, and either (a) are derived from faunas that evolved *in situ* or (b) evolved through a mixture of local evolution and faunal enrichment from neighboring regions. These regions were either non-forest regions around *Nothofagus* forests (as in South America, Vuilleumier 1985), or forests of a different type nearby (as in many areas of the SW Pacific, Kikkawa 1984). We do not yet possess for birds, data such as those reported for bats by Pierson et al. (1986), showing a New Zealand-South American link.

ACKNOWLEDGEMENTS

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CONCLUDING REMARKS: THE METHODOLOGY OF RECONSTRUCTING THE PAST

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We have chosen to conclude our symposium with a short precis of each of the five papers presented at the Congress.

In the contribution entitled "Molecular Studies of New Zealand's Extinct Ratites" (to be published elsewhere), A. Cooper, G.K. Chambers, A.C. Wilson, and S. Paabo compared the mitochondrial DNA from 5 genera of extinct moas (Dinornithidae and Emeidae, extracted from mummified tissue) to corresponding nucleotide sequences in the 3 extant species of kiwis (Apterygidae). The latter have previously been considered to be closely related to moas. A phylogeny based on the aforementioned sequences suggests that the New Zealand ratites (kiwis and moas) are not as closely related as was previously reported.

In "An Overview of the Taxonomy, Fossil History, Biology and Extinction of Moas", Worthy reviews the fossil record of the Dinornithiformes, an order of medium-sized (15 kg) to very large (270 kg), wingless New Zealand endemics comprising 2 families, 11 species, and 6 genera. The fossil record of moas is, so far as known, restricted to the late Pliocene and Quaternary. Worthy relates sexual size dimorphism in moas to their large absolute size and discusses the probable diet of moas (twigs, leaves and fruit) based on analysis of gut contents, bill morphology, and paleoenvironments. Moas lived in a stable habitat prior to human colonization of New Zealand about 1000 years B.P. Inferred paleoenvironments of moas include lowland forest, grassland-shrubland-forest mosaics, and subalpine habitats.

In a paper entitled "Paleobiology and Relationships of the Giant Groundbird *Diatryma* (Aves: Gastornithiformes)", Andors analyzes the trophic and locomotory adaptations, and probable phylogenetic affinities of this enigmatic genus of flightless birds. Four species of *Diatryma* are currently recognized and placed in a monotypic family Diatrymidae, with a record confined to the Eocene of North America and Europe. The European diatrymids and the related Gastornithidae (8 species in 2 genera) from the Paleocene and Eocene of Eurasia need to be revised. However, the postulated close relationship between the Diatrymidae and the Gastornithidae would justify the traditional assignment of these families to an order Gastornithiformes. The customary placement of *Diatryma* in or near the Gruiformes is probably invalid. Restudy of *D. gigantea* suggests that the Gastornithiformes are the sister-group of the Anseriformes, and that the Galliformes are the sister-group of the Gastornithiformes + Anseriformes. *Diatryma* appears to have been a pedestrian herbivore, not a cursorial predator as usually assumed.

In a contribution entitled "Zoogeographical Relationships of the Eocene Avifauna from Messel (Germany)", Peters divides the spectacular Middle Eocene fossil avifauna from Messel into three zoogeographical groups. In the first group belong the taxa known only from Messel. The second group contains taxa (e.g. the Messelornithidae, Cariamidae, and the early flamingo, *Juncitarsus*) that also occur at contemporaneous sites in Europe and North America. The third group includes taxa such as the Palaeotididae, Phorusrhacidae, and Podargidae that are shared with coeval sites in Europe and with the fossil or Recent avifaunas of South America or SE Asia, but which are as yet unknown in North America. This zoogeographical classification of the Messel avifauna suggests that some Group 3 taxa will be found in the African record.

In "Reconstructing the History of *Nothofagus* Forest Avifaunas", Vuilleumier & Kikkawa attempt to trace the history of the approximately 323 species of birds that inhabit forests dominated by southern beeches (*Nothofagus*, Fagaceae). These forests are restricted to a few temperate and tropical regions in the Southern Hemisphere. Since the fossil and Recent distribution of *Nothofagus* suggest a Gondwanan origin for the genus, it may be asked whether *Nothofagus* forest birds had a similar origin. New Zealand is the only *Nothofagus* containing area with an appreciable avian fossil record, but that is limited to the Quaternary. The results of an analysis of the distribution and systematic relationships of Recent taxa are not altogether conclusive, but some interesting patterns emerge. Some taxa (e.g. Apterygidae and Acanthisittidae), termed old autochthons, have apparently had a long Cenozoic history in or near their present centers of distribution. These older faunal elements are confined to one side of the Pacific basin or the other. Other taxa, termed derived autochthons (e.g. *Hemiphaga* and *Campephilus*), have probably occupied *Nothofagus* forests since the mid or late Cenozoic. In the Late Pleistocene or Holocene, other bird taxa have probably dispersed by natural means to *Nothofagus* forests from nearby source areas (e.g. *Cathartes*, *Phylloscopus*, *Zoothera*, and *Gerygone*). Finally, some taxa have recently been imported by man (species in the genera *Turdus*, *Prunella*, *Fringilla*, and *Acanthis*). There is as yet little evidence for a Gondwanan history of any *Nothofagus*-associated birds.

The diversity of approaches, taxa, and methodologies used by the participants in this symposium exemplifies the broad spectrum of research strategies used in the late 80s and early 90s in avian paleontology and in reconstructing the past. Symposia dealing with avian paleontology at earlier IOCs were much more concerned with taxonomic descriptions or faunal lists. Our field has clearly progressed substantially in the last couple of decades.

In closing, the convenors would like to thank W.J. Bock and M.J. Williams for their assistance in resurrecting Symposium 6. The contributors also deserve our special vote of thanks for their willingness to submit their papers according to an accelerated schedule.

SYMPOSIUM 7

**MODERN BIOCHEMICAL APPROACHES
TO AVIAN SYSTEMATICS**

Conveners R. M. ZINK and P. R. BAVERSTOCK

SYMPOSIUM 7

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INTRODUCTORY REMARKS: MODERN BIOCHEMICAL APPROACHES TO AVIAN SYSTEMATICS

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Systematists study geographic variation, species limits and speciation, phylogenetic relationships (the cornerstone of all comparative biology), and biogeography. Advances in methods of gathering and analyzing biochemical genetic data have revitalized systematics, and in this symposium molecular methods in avian systematics are showcased. To analyze genetic differences among sibling species, Gelter and Tegelstrom use a multi-dimensional approach including protein electrophoresis, mitochondrial DNA (mtDNA) restriction endonuclease cleavage analysis, and analysis of repeated DNA segments. Johnson and Cicero illustrate the use of mtDNA sequence data in analysis of geographic variation. Baverstock and colleagues (Schodde, Christidis, Krieg, Sheedy) use immunological comparisons to make phylogenetic inferences. Arctander reviews applications of the polymerase chain reaction (PCR) and direct sequencing of mtDNA in addressing a number of systematic questions, including the phylogenetic affinities of a seemingly atypical specimen. Lastly, Edwards, Quinn, and Wilson provide further evidence of the value of the PCR technique and sequencing information in questions concerning avian systematics and molecular evolution.

A variety of molecular methods exist for studying questions at various tiers of taxonomic resolution. Clearly, we have achieved one long-strived-for goal, that of being able to sequence directly the hereditary message, DNA. What better way to unravel the evolutionary thread of heredity than by having direct access to the blueprint itself? Although direct sequencing of DNA will become routine, it is also apparent that other molecular techniques will retain their value in avian systematics. In this symposium, these methods are reviewed and exciting new findings presented.

GENETIC DIFFERENTIATION BETWEEN TWO CLOSELY RELATED FLYCATCHER SPECIES (MUSCICAPIDAE)

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ABSTRACT. The two old world flycatcher species, the Pied and the Collared Flycatcher are ecologically and behaviourally similar except for their song. The species have a predominantly allopatric distribution but hybridize in areas of geographic overlap. The genetic differentiation between the two species detected by protein electrophoresis was low (Nei's genetic distance 0.0006), and no species-specific alleles were found. Repetitive sequences in nuclear DNA investigated by restriction enzymes were also similar. A comparison of restriction fragment differences in mitochondrial DNA, however, showed a sequence divergence of 10% between the species. The karyotypes of the two species are similar, both possessing 80 chromosomes. Studies of hatching success in combination with DNA-fingerprinting studies of parentage showed that female interspecific hybrids are sterile whereas hybrid males are fertile. Asymmetrical hybrid fertility allows nuclear but prevents mitochondrial gene flow between the species. These results demonstrate the advantage of using a multi-methodological approach for analyzing genetic divergence and speciation.

Keywords: Pied Flycatcher, Collared Flycatcher, protein electrophoresis, repetitive sequences, mitochondrial DNA, DNA fingerprinting, hybridization.

INTRODUCTION

Several biochemical methods are available for studies of systematic and evolutionary problems. Usually, only one method is used to solve a certain problem and conclusions thus are dependent on the limitations or resolution of that particular method. Different methods can yield incongruent results and have generated discussions concerning which technique best reveals evolutionary events. Each method may, however, give information about different evolutionary events of the species investigated.

According to the Neo-Darwinian theory, speciation involves the establishment of reproductive isolation between populations during a period of geographic isolation (Mayr 1963). Because each taxonomic group has a unique evolutionary history, different characters in morphology, ecology, behaviour, or different parts of the genome, such as unique or repetitive DNA or chromosomes, will differentiate before, during and after a speciation event. The interpretation of the results of a particular technique thus depends on how these characters have evolved in that particular species or taxonomic group.

In this report we show that seemingly contradictory results obtained by different biochemical methods can have a biological explanation. We studied two closely related Old World flycatchers of the family Muscicapidae, the Pied Flycatcher *Ficedula hypoleuca* (Pall.) and the Collared Flycatcher *F. albicollis* (Temm.), which are very similar with respect to morphology and plumage characters. Both species have sexually dimorphic plumages. Females from both species are dull brown and white and are

almost indistinguishable. Males of both species are black and white but the Collared Flycatcher has a characteristic white collar and rump. All Collared Flycatcher males are black, whereas Pied Flycatcher males vary in plumage from jet black to female-like brown (Dorst 1936). This variation in colour is partly age dependent but also varies geographically in a northwest-southeast cline (Winkel et al. 1970, Roskaft et al. 1986).

ECOLOGICAL SIMILARITY

The Pied Flycatcher has its main breeding area in the northwestern part and the Collared Flycatcher in the southeastern part of Europe (Wallin 1986). The species distributions overlap in central and eastern Europe and on the Baltic islands of Gotland and Oland. The taxonomic rank of these two flycatchers has been unclear but they are now considered as semispecies, with a postulated origin in different refugia during Pleistocene glaciations (Haartman 1949). Both species are migratory with allopatric overwintering areas in central Africa.

Ecological aspects of breeding, foraging and mate choice are discussed by Alerstam et al. (1978), Roskaft & Jarvi (1983), Askemo (1984), Alatalo et al. (1986), and Gottlander (1987). Although most breeding pairs appear to be monogamous in both species, up to 35% of the males are polygynous by being polyterritorial (Alatalo et al. 1982c, Alatalo & Lundberg 1984). Twenty-nine percent of the observed copulations in Pied Flycatcher were found to be extra-pair copulations (EPC) (Alatalo et al. 1987) and the heritability of tarsus length indicates that 18% of the Pied Flycatcher nestlings and 21% of the Collared Flycatcher nestlings were fathered by non-mate males (Alatalo et al. 1989). These observations were confirmed by DNA fingerprinting (Tegelstrom & Gelter unpubl.), indicating a frequency of 24% extra-pair fertilization (EPF) among Pied Flycatcher nestlings.

ETHOLOGICAL SIMILARITY

Most behaviours involved in pair formation and reproduction appear to be similar between the Pied and the Collared Flycatcher (Haartman & Lohrl 1950). Of the 15 homologous vocalizations described, only two differ between the species, the full song and a low intensity alarm call (Haartman & Lohrl 1950, Lohrl 1955, Gelter 1987, Wallin 1987).

Prezygotic isolation mechanisms involved in separating the Pied and Collared Flycatcher seem to be weakly developed and mainly consist of differences in song and male plumage. Despite a weak prezygotic isolation, matings seem to be assortative within each species. The frequency of mixed pairs is lower than expected by random matings between the species (Alatalo et al. 1982a, 1990).

HYBRIDIZATION

The Pied and Collared Flycatcher hybridize in areas of distributional overlap (Lohrl 1950, 1955, Alerstam et al. 1978, Alatalo et al. 1982a, Kral 1988, Gelter 1987, Gelter et al. 1991). Male hybrids have intermediate plumage characters with the collar more

or less broken in the neck by grey or black feathers. Hybrid males sing like the Collared Flycatcher and have alarm calls of both species (Gelter 1987). Female hybrids also give the alarm calls of both species. Mixed pairs show the same reproductive success as pure species pairs whereas hybrids seem to be less successful (Alerstam et al. 1978, Alatalo et al. 1982a,b).

The presence of hybrids in areas of distributional overlap indicates incomplete reproductive isolation. Whether this incomplete isolation leads to introgression was studied among hybrids of both sexes on the island of Gotland (Gelter et al. 1991). Hatching success of 25 female and 37 male hybrids, each mated with a "pure" species mate, was in agreement with Haldane's rule (Haldane 1922), which states that the heterogametic sex shows a higher degree of sterility than the homogametic sex when two genetically differentiated populations hybridize. None of the female hybrids (ZW) hatched any nestlings, thus appearing sterile, whereas male hybrids (ZZ) had almost normal hatching success (see also Alatalo et al. 1990).

The possibility that females can compensate matings with hybrid males by EPC (Buitron 1983, Loman et al. 1988) makes the observed hatching success in nests of male hybrids unreliable as an estimate of true hybrid fertility. We therefore checked the paternity of hybrids involved in parental care by DNA-fingerprinting (Gelter et al. 1991) using two minisatellite probes. We found that among seven breeding male hybrids, six were truly fertile. One male hybrid raised only unrelated nestlings, and extra-pair fertilization (EPF) was found in two additional nests. The frequency of EPF-nestlings in these hybrid families was 25%, a frequency similar to that found in the Pied Flycatcher (24%, Gelter & Tegelstrom in prep.).

GENETIC SIMILARITY

Karyotype

Avian karyotypes have been described as being conservative in number and morphology (Tegelstrom & Rytman 1981), but this may not be true for all taxa (Christidis 1983, Van Dongen & De Boer 1984), especially when different banding techniques are applied (Stock & Bunch 1982). G- and C-banding of metaphase chromosomes prepared from bone marrow of six individuals each of Pied and Collared Flycatchers, show that the two species possess nearly identical karyotypes (Andayani et al. 1991). Both species have a karyotype with $2n=80$, comprised of seven pairs of macrochromosomes and 33 pairs of microchromosomes. G- and C-banding of chromosomes did not reveal any differences between the species. The karyotypes of the two species differ only in the number of small metacentric chromosomes, Collared Flycatcher having five pairs and Pied Flycatcher four pairs. This difference between the two species has likely originated by a pericentric inversion. The very similar karyotypes of the two species suggest that female hybrid sterility cannot be explained by chromosomal differences.

Protein electrophoresis

Protein electrophoresis has often been used to estimate relatedness between taxonomic groups (Corbin 1983, Matson 1984). Although birds show less genetic divergence at all taxonomic levels compared to other vertebrates, the technique is valuable for estimating genetic differentiation (Barrowclough 1983, Avise 1983).

To estimate the genetic differentiation in nuclear genes, we used protein electrophoresis to survey 170 Pied Flycatchers and 63 Collared Flycatchers (Gelter et al. 1989). Among the 35 loci investigated the proportion of polymorphic loci was 11.5% for the Pied Flycatcher and 8.6% for the Collared Flycatcher, and the average heterozygosity was 0.8% and 1.4%, respectively. Both the proportion of polymorphic loci and the mean heterozygosity were lower in these species compared to those for other avian species (Evans 1987). No fixed allelic differences were found between the species. However, among eight variable loci, three showed significant allele frequency differences. The relative gene diversity (G_{ST}) between the species was low with 97.6% of the variation present within each species. Nei's genetic distance (D) was 0.0006, much lower than that between other congeneric passeriform species ($D=0.044$, $n=84$) and in the range of local conspecific passeriform populations ($D=0.0024$, $n=113$, Ankney et al. 1986).

The low genetic differentiation between the two flycatcher species (corresponding to a few thousand years since divergence, Nei 1975), can be explained either by a recent speciation without genetic changes in isoenzymes, or by ongoing or recent hybridization with introgression between the species (Gelter et al. 1989). The extent of observed hybridization (2-4% hybrids of the breeding population) on the islands in the Baltic sea (Alerstam et al. 1978, Alatalo et al. 1982a) would be enough to maintain the same neutral alleles in the two species in areas of sympatry (Kimura & Ohta 1971).

Repetitive sequences

Changes in repetitive DNA sequences may be involved in speciation (Flavell 1982). Differences in repetitive sequences may disturb chromosome pairing, gene expression or chromosome behaviour during hybrid meiosis (Flavell 1982). By digestion of high-molecular-weight genomic DNA with five restriction endonucleases, we investigated repetitive sequences in the Pied and Collared Flycatcher, and in the Blue and Great Tit *Parus caeruleus* and *P. major* (L.) (Gelter & Tegelstrom 1990). The two flycatcher species showed no difference in their repetitive sequences for all five restriction enzymes. The two tit species showed no repetitive fragments for one restriction enzyme and differed for the other four restriction enzymes. No repetitive fragments were shared between the flycatcher and tit species.

Due to the close similarity in repetitive sequences between the two flycatcher species, repetitive sequences do not appear to be involved in the infertility of the flycatcher female hybrids. This is in agreement with their close similarity in nuclear genes revealed by the isozyme studies.

GENETIC DISSIMILARITY

Mitochondrial DNA

Genetic variation in mitochondrial DNA (mtDNA) restriction sites has provided an important perspective on evolutionary problems (Shields & Helm-Bychowski 1988). Studies of genetic differences between avian species or subspecies (Kessler & Avise 1985, Mack et al. 1986, Oveden et al. 1987, Zink & Avise 1990) indicate, as with protein studies, that birds in general exhibit less divergence than do other vertebrate taxa. The maternally inherited mtDNA behaves as a clonally transmitted marker, and

reflects founder or rare immigration events more directly than variation in nuclear DNA (Wilson et al. 1985). Therefore investigations of variation in mtDNA seem to be a more powerful approach than isozyme electrophoresis in studies of closely related avian species.

By cleavage of mtDNA with eight restriction enzymes covering about 5% of the mtDNA genome, we compared mtDNA of Pied and Collared flycatchers (Tegelstrom & Gelter 1990). We found a sequence divergence of about 10% between the two species of flycatchers which corresponds to about 5 million years since clonal divergence accepting a rate of 2% per million years (Brown et al. 1982, Shields & Wilson 1987a). This large genetic distance in mtDNA indicates a clonal separation between the flycatcher species predating the origin of most extant passeriform species, assumed not to be older than 1 Myr (Brodkorb 1971). The observed divergence between the Pied and Collared Flycatcher is considerable higher than the mitochondrial DNA divergence usually found among avian species ($p=5.2\%$, $n=65$) and within the range of avian genera (mean $p=8.9\%$, $n=7$) (Tegelstrom & Gelter 1990).

The high mtDNA divergence contrasts with the low level of nuclear divergence revealed by different techniques. The pattern of divergence between the two flycatcher species thus deviates from the common pattern of genetic differentiation in nuclear and mitochondrial genomes found in birds (Tegelstrom & Gelter 1990). One possible explanation for the high divergence in mtDNA between the flycatcher species could be a higher mutation rate compared to other avian species. Intraspecific mtDNA variation among 20 Pied Flycatchers from four localities revealed a pairwise divergence of $0.35\pm 0.16\%$ (Tegelstrom et al. 1990) which is similar to that found among other bird species (Shields & Wilson 1987b, Tegelstrom 1987a, Ball et al. 1988, Avise & Nelson 1989, Zink & Avise 1990). Thus, there seems to be no indication of an exceptional mutation rate of flycatcher mtDNA.

An explanation for high mtDNA differentiation compared to nuclear genes could be a transfer of mtDNA from a third species to one of the flycatchers during a period of hybridization, probably during the Pleistocene interglacial periods (Tegelstrom & Gelter 1990). Natural transfer of mtDNA between non-avian species has been described (Tegelstrom 1987b) but so far, not between avian species. As the probability to hybridize increases when a species becomes rare (Short 1969), and these flycatchers seem to have undergone bottlenecks (Gelter et al. 1989, Tegelstrom et al. 1990), transfer of mtDNA between one of the flycatchers and a third species might have occurred.

CONCLUSIONS

Pied and Collared flycatchers are almost undifferentiated in their nuclear genomes, which may be a consequence of introgressive hybridization through fertile male hybrids. Despite ongoing hybridization, male morphological species-specific characters and loci involved in female hybrid sterility persist in sympatric populations of both species, indicating selection preserving species-specific alleles, probably in just a few loci. Persistence of distinctive morphological characters in spite of hybridization has been proposed by Carson et al. (1989) as a consequence of sexual selection preserving characters used in mate choice.

Despite introgressive hybridization, the two flycatcher species are highly differentiated in their mitochondrial genomes. The persistence of the difference between the Pied and the Collared Flycatcher in the maternally inherited mtDNA may be due to the fact that female hybrids are sterile. The unusually high mtDNA differentiation may be an effect of a former hybridization with a third, less closely related species. A comparison of mtDNA from several potential species could clarify this possibility. The observed low nuclear differentiation between the Pied and Collared Flycatchers should place the two species in an intraspecific taxonomic position, whereas the high mtDNA differentiation indicates an intergeneric taxonomic position. These contradictory conclusions result from different biological events during the isolation periods in Pleistocene refugias which have led to divergence in some but not in other characters and genes. Our results illustrate the importance of collecting information by different methods revealing genetic differentiation on different levels of genomic organization, from base mutations in nuclear and mtDNA to morphology and behaviour.

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MITOCHONDRIAL DNA SEQUENCE VARIABILITY IN TWO SPECIES OF SPARROWS OF THE GENUS *AMPHISPIZA*

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ABSTRACT. After amplification of mtDNA with the polymerase chain reaction (PCR), we directly sequenced 288 base pair fragments in the cytochrome b region from specimens representing three subspecies of the Sage Sparrow (*A. belli belli*, *A. b. canescens*, and *A. b. nevadensis*) and two subspecies of the Black-throated Sparrow (*A. bilineata deserticola* and *A. b. opuntia*). These abundant songbirds inhabit arid brushlands in western North America. *A. b. belli* allies most closely with *A. b. canescens* rather than with *A. b. nevadensis*. In pairwise comparisons, average percent nucleotide difference varied from 0.1% (within populations), 0.4% (between populations of the same subspecies), and 0.6% (subspecies within species), to 10.9% (between species). The trend continued in interfamilial (13.9 - 17.4%) and interordinal (19.7%) comparisons. The ratio of transversions to transitions also increased over the same taxonomic range. Nucleotide sequence differences and allozymic differences (Nei's *D*) between the same populations were very highly correlated ($r = .98$; Mantel test). mtDNA base variability in cytochrome b can be useful in assessing relationships at various taxonomic levels, down to and including populations.

Keywords: Sage Sparrow, *Amphispiza belli*, Black-throated Sparrow, *Amphispiza bilineata*, mtDNA nucleotide sequence variation, cytochrome b, molecular evolution.

INTRODUCTION

The Sage Sparrow *A. belli* and the Black-throated Sparrow *A. bilineata* nest abundantly in arid brushlands in western North America. The former species is represented by three strongly-characterized subspecies (*A. b. belli*, *A. b. canescens*, *A. b. nevadensis*) that differ in size, coloration, habitat preference, and migratory tendency (Table 1) in the continental western United States. Two other named subspecies occur on San Clemente Island, California *A. b. clementeae* and in central Baja California, Mexico *A. b. cinerea*, respectively; we do not treat them here. The Black-throated Sparrow, in contrast, illustrates less striking geographic variation in color and size. An examination of comparative levels of genetic variation within and among populations, subspecies, and species of these undoubted congeners is therefore of interest.

Johnson and Marten (in prep.) recently completed an extensive survey of allozymic and morphologic variation in breeding populations of the Sage Sparrow in the western United States. Here we extend that genetic analysis with data on nucleotide sequence variability in a portion of the cytochrome b region of mitochondrial DNA (mtDNA) for selected samples representing the three continental subspecies. Homologous sequences for two subspecies of the Black-throated Sparrow (*A. bilineata deserticola*, *A. b. opuntia*) are offered for comparative purposes.

TABLE 1 - Comparison of morphologic, ecologic and behavioral features of three subspecies of the Sage Sparrow *Amphispiza belli*.

Taxon	Size	Color	Habitat ^a	Migratory Tendency	Nesting Distribution ^b
<i>A. b. belli</i>	Small	Dark	<i>Adenostoma</i>	Sedentary	Fragmented
<i>A. b. canescens</i>	Small	Pale	<i>Atriplex</i>	Short distance	Fragmented
<i>A. b. nevadensis</i>	Large	Pale	<i>Artemisia</i>	Short distance	Continuous

^aThe principal habitat is given. *A. b. belli* breeds also in coastal sage habitats in southern California, *A. b. canescens* nests in *Ephedra* in parts of the northern San Joaquin Valley, and *A. b. nevadensis* occasionally breeds in brushland where Big Sagebrush *Artemisia tridentata* is mixed with shadscale *Atriplex*.

^b*A. b. belli* and *A. b. canescens* probably do not intergrade, despite statements to the contrary in Grinnell & Miller (1944:501). Although their required habitats are separated by only a few airline miles, the strong habitat disjunction and concomitant climatic break may preclude contact by individuals in breeding condition. Furthermore, although Grinnell & Miller (1944:500) reported intergradation between *A. b. canescens* and *A. b. nevadensis* in the northern end of Owens Valley, Johnson & Marten (in prep.) could not find corroborating evidence.

MATERIALS AND METHODS

Specimens

Liver tissue of Sage Sparrows and Black-throated Sparrows was frozen at -196°C in liquid nitrogen within 1-4 hr after collection in the field prior to permanent storage at -70°C in Berkeley, California. Two individuals from each of two localities (Figure 1) representing each of the three subspecies of Sage Sparrow were sequenced. One specimen from each of the two subspecies of Black-throated Sparrow was analyzed. Thus, we sequenced a total of 14 individuals of the genus *Amphispiza*.

DNA extraction

DNA was extracted from 15-20 mg frozen liver tissue by digesting the tissue in 500 µl lysis buffer (50 mM Tris HCL, pH 8.0; 50 mM EDTA, pH 8.0; 1% SDS; 100 mM NaCl; 1% 2-mercaptoethanol) and 11 µl proteinase K at 55°C with gentle mixing for 15-20 hr. RNase A (5.5 µl) was added to each sample 1 hr before the end of incubation. The DNA was purified by extracting once with phenol (pH 8.0), once with phenol:SEVAG (1:1), and once with SEVAG (24 chloroform:1 isoamyl alcohol). Ethanol precipitation was used to concentrate the DNA. Samples were stored in 1x Tris EDTA (pH 8.0) at 4°C. One control lacking tissue was carried through the procedure to check for contamination. Protocols for preparing stock solutions for both DNA extraction and amplification followed Maniatis et al. (1982).

Amplification of DNA

Two primers (MVZ3, MVZ4) targeted to a 366 base pair (bp) region of cytochrome b (Kocher et al. 1989:139) were used for amplification of both light and heavy strands using the polymerase chain reaction (PCR) (Marx 1988, White et al. 1989). Double-stranded (ds) amplifications were performed in 25 µl reactions containing 12.5 µl of the target DNA and a mixture with final concentrations of 67 mM Tris (pH 8.8), 2 mM MgCl₂, 16.7 mM ammonium sulfate, 10 mM β-mercaptoethanol, a dNTP mix at 0.75 mM, each primer at 1 µM, 0.625 units of *Thermus aquaticus* (Taq) polymerase (Perkin Elmer-Cetus), and double-distilled water. Singlestranded (ss) reactions were

performed in 50 μ l volumes containing 10 μ l of the target DNA, 15 μ l of double-distilled water, and 25 μ l of the PCR mixture. The PCR solution was the same for ss reactions except that a 50:1 ratio of one primer (10 μ M) to the other (0.2 μ M) was used. This ratio was reversed when amplifying the complementary strand. Reaction volumes were layered with 2 drops of mineral oil to prevent evaporation during heating. Samples were placed in a Techne programmable heating block (Perkin Elmer-Cetus) for thermal cycling. Each PCR cycle consisted of denaturation for 2 min at 94°C, annealing for 1 min at 55-62°C, and extension for 1 min at 72°C. The number of cycles varied from 26 (ds reactions) to 30 (ss reactions). Each sample was replicated at least

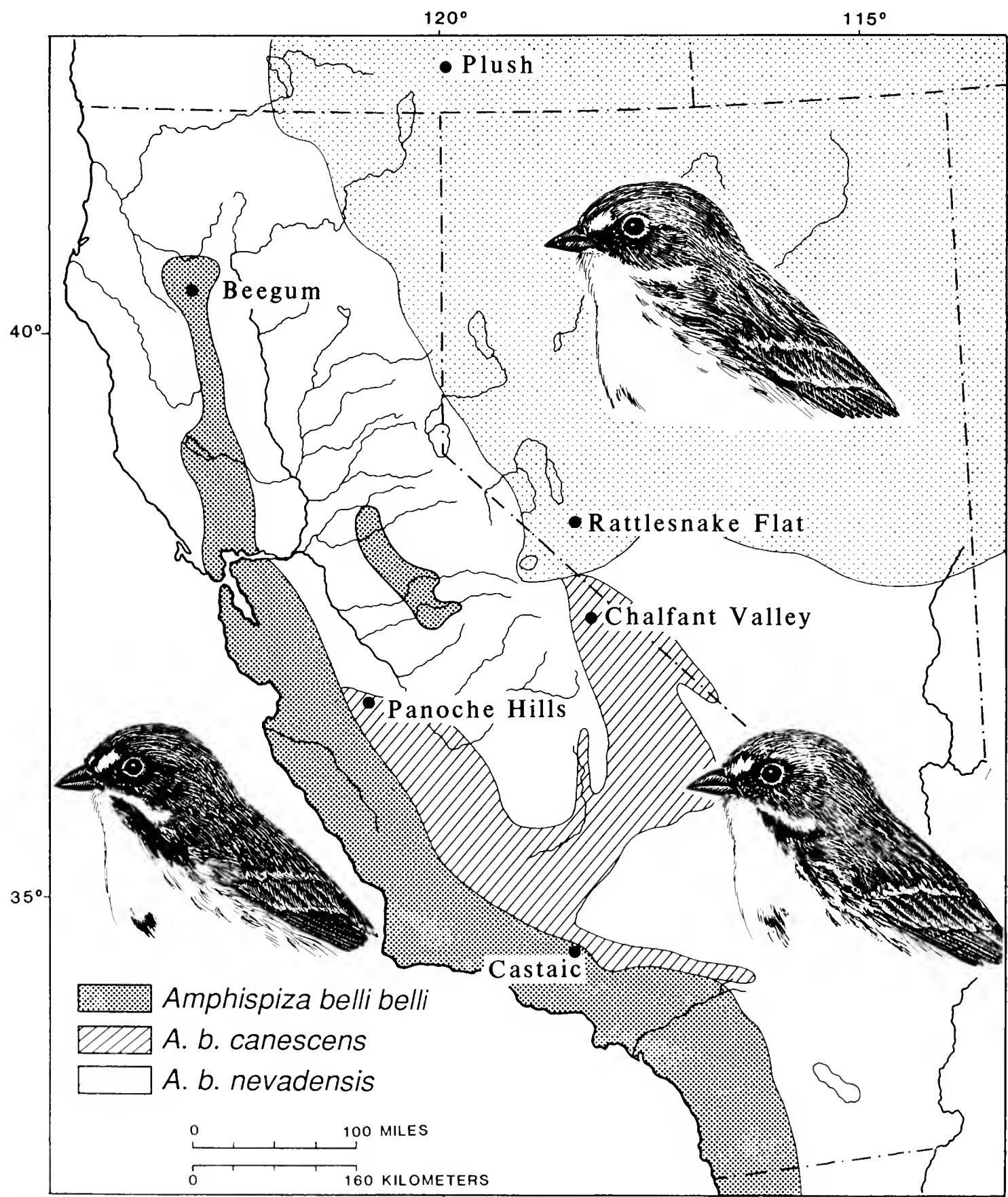


FIGURE 1 – Approximate breeding distribution of three subspecies of the Sage Sparrow in California, Nevada, and outhern Oregon. The six localities from which samples were chosen for sequencing are shown. The map is based on Grinnell & Miller (1944:500) and American Ornithologists' Union (1957).

once, and two controls were included in each set of reactions to insure against contamination.

Amplified ds products were resolved by electrophoresis in a 4% NuSieve agarose gel in 1x Tris Borate EDTA and stained with ethidium bromide to visualize the DNA. Agarose plugs excised from ds bands and melted in 250 µl distilled water were used as templates for the ss reactions. Free nucleotides and salts were removed from the ss products by centrifugation dialysis. The DNA was concentrated in 20 µl of distilled water and stored (4°C) until sequencing.

Direct sequencing of amplified products

Sequencing reactions were performed using 7 µl of the DNA template and the primer that was limiting in the ss amplifications. Sequencing was done with a commercial kit (Sequenase, US Biochemical Corp.) according to the Sanger dideoxy chain-termination method (Sanger et al. 1977). The resulting products were resolved in 6% polyacrylamide-8.3 M urea gels and autoradiographed. Samples were sequenced repeatedly until unambiguous sequences were obtained for each specimen. Sequences were read, aligned, and translated with the computer program ESEE (Cabot & Beckenbach 1989).

Mantel test

The relationship between average nucleotide difference and Nei's (1978) genetic distance (D) was assessed with a Mantel (1967) test using the program GENESYS.EXE.3.2 (MANTEL.COM 1.4) written by Kendall W. Corbin.

RESULTS

DNA sequence variation in *Amphispiza*

MTDNA GENOTYPES. Sequences of the 14 specimens ranged in length from 288 to 343 bp ($x = 299$ bp). Translation and alignment of these sequences identified 288 shared homologous nucleotide positions in all individuals. We classified these sequences into six distinct genotypes (Table 2).

INTRASPECIFIC MTDNA VARIATION. Population differences within each of the three subspecies of Sage Sparrow were slight (Table 2). Only two changes were detected when comparing individuals from the same population or from another population representing the same subspecies. In both instances (Genotypes 2 and 4), the differences occurred at a single nucleotide unique at that site among the 14 sequences. The mutation in Genotype 2, however, was especially significant in that it resulted in an amino acid change from Asparagine (Asn) to Aspartic acid (Asp).

Divergence among the three subspecies of Sage Sparrow was surprisingly low in light of their strong phenotypic, ecologic, and behavioral differences (Table 1). Nucleotide differences between populations representing different subspecies varied from 0 to 4 (Table 2), all of which were transitions (Table 3). Most of those changes, with the exception of that in Genotype 2, occurred at silent sites in the third position of the codon. Subspecific differences were most pronounced between *A. b. belli* and *A. b. nevadensis*. Sequences of *A. b. canescens* showed a split affinity (Table 2): individuals from the Panoche Hills had the same genotype as *A. b. belli* (Genotype 1), two

whereas those from Chalfant Valley allied most closely to *A. b. nevadensis* (Genotypes 3 and 4). This result suggests that populations of Sage Sparrows in the northern Owens Valley are most closely related to those in the Great Basin (*A. b. nevadensis*) rather than to those in the Mohave Desert (*A. b. canescens*), where traditionally they have been placed (Grinnell and Miller 1944:500).

TABLE 2 - Variable mtDNA codons^a in a 288 base pair sequence of cytochrome b^b in six genotypes (G1-G6) representing 12 individuals of the Sage Sparrow and two individuals of the Black-throated Sparrow.

		40	43	44	46	47	49	50	53	60	65	66	
Genotypes ^c		Ile	Ile	Thr	Ile	Val	Gly	Leu	Ala	Thr	Ser	Ser	
G1		ATC	ATC	ACC	ATC	GTT	GGC	CTC	GCC	ACC	TCC	TCC	
G2		
G3		
G4		
G5		<u>G</u> ^dT	..T	..T	<u>A</u> .C	..A	..TT	^eT	
G6		<u>G</u> .T	..T	..T	...	<u>A</u> .C	..A	..T	..TT	
		68	70	75	76	79	81	84	98	100	103	104	
		Ala	Thr	Gln	Phe	Leu	Arg	His	His	Gly	Ile	Tyr	
G1		GCC	ACA	CAA	TTT	CTT	CGC	CAC	CAT	GGC	ATC	TAT	
G2		
G3	C	
G4	C	
G5		..T	.. <u>I</u> .	<u>A</u>C	..C	..T	..T	..C	..A	<u>C</u>C	
G6		..T	.. <u>I</u> .	<u>A</u>C	..C	..T	..T	..C	..A	<u>C</u>C	
		105	106	110	112	114	116	118	119	120	127	129	131
		Tyr	Gly	Asn	Glu	Trp	Val	Ile	Ile	Leu	Thr	Phe	Gly
G1		TAC	GGC	AAC	GAG	TGG	GTT	ATC	ATT	CTC	ACC	TTC	GGA
G2		<u>G</u>
G3	G
G4	TG
G5		..T	..T	<u>I</u>A	..A	<u>A</u> ..	<u>G</u>C	..A	..A	..T	...
G6		..T	..T	<u>I</u>A	..A	<u>A</u> ..	<u>G</u>CA	..T	...

^aCodons were translated and numbered according to the sequence of cytochrome b in the chicken *Gallus gallus domesticus* (Desjardins & Morais 1990). Abbreviations for the amino acid are given above each codon. Because there is an extra codon near the start of cytochrome b in the chicken that is not present in either the human (Anderson et al. 1981) or mouse (Bibb et al. 1981) sequences, codon numbers do not correspond exactly to those given in Kocher et al. (1989). For example, codon 40 in cytochrome b of the chicken corresponds to codon 39 in the homologous human sequence.

^bThe sequenced fragment is homologous to base pairs 15,004-15,291 in the mtDNA of the chicken (Desjardins & Morais 1990). The first variable site in *Amphispiza* occurred at 15,010 bp.

^cOccurrence of various genotypes: No. 1 - *A. belli belli*: Beegum, NKJ 5305 & 5306; Castaic, NKJ 5568; *A. b. canescens*: Panoche Hills, NKJ 5131 & 5132. No. 2 - *A. b. belli*: Castaic, NKJ 5569. No. 3 - *A. b. canescens*: Chalfant Valley, NKJ 4047 & 4048; *A. b. nevadensis*: Rattlesnake Flat, NKJ 4035 & 4036; Plush, NKJ 5476. No. 4 - *A. b. nevadensis*: Plush, NKJ 5475. No. 5 - *A. bilineata deserticola*: Nevada, NKJ 5622. No. 6 - *A. bilineata opuntia*: Oklahoma, CSW 737.

^dUnderlined nucleotides signify an amino acid change.

^eBoth mtDNAs of *A. bilineata* have a single guanine inserted between codons 64 and 65 that is not found in any of the 12 *A. belli*.

TABLE 4 – Average percent nucleotide difference among sequences of a 239-288 base pair segment of cytochrome b from taxa differentiated at several taxonomic levels.^a

Taxonomic level	Number of pairwise comparisons	Average percent nucleotide difference ^b	Range	Average transition: transversion bias ^c
Intrapopulation ^d	6	0.1	0.0 - 0.4	0.3:0
Interpopulation within subspecies	12	0.4	0.0 - 1.0	1:0
Intraspecific (subspecies)	49	0.6	0.0 - 1.7	2:0
<i>A. belli</i> ^e	48	0.6	0.0 - 1.0	2:0
<i>A. bilineata</i>	1	1.7	–	4:1
Interspecific congeners ^f				
<i>A. belli</i> v <i>A. bilineata</i>	24	10.9	10.8 - 11.1	25:7
Interfamilial				
<i>Amphispiza</i> v <i>Corcorax</i>	14	13.9	13.4 - 15.9	17:17
<i>Amphispiza</i> v <i>Pomatostomas</i>	56	17.4	15.5 - 18.8	22:19
Interordinal				
<i>Amphispiza</i> v <i>Gallus</i>	14	19.7	19.1 - 20.1	26:31

^a Comparisons within *Amphispiza* and between *Amphispiza* and *Gallus* (Desjardins & Morais 1990) are based on 288 bp sequences. Interfamilial comparisons between *Amphispiza* and either *Pomatostomas* or *Corcorax* are based on 239 bp sequences (Kocher et al. 1989) homologous to a segment of the *Amphispiza* sequences. Four species of *Pomatostomus* (*P. ruficeps*, *P. superciliosus*, *P. temporalis*, *P. isidori*) and *Corcorax melanorhamphos* (Kocher et al. 1989) were used in the interfamilial comparisons.

^b Calculated as the average number of pairwise nucleotide differences (transitions + transversions) divided by the total number of bases compared.

^c Calculated as the number of transitions:transversions averaged over all pairwise comparisons.

^d Pairwise comparison of two individuals of *A. belli* from each of six populations (Beegum, Castaic, Panoche Hills, Chalfant Valley, Rattlesnake Flat, Plush).

^e Pairwise comparison of two populations (two individuals from each) representing three subspecies of the Sage Sparrow (*A. b. belli*, *A. b. canescens*, *A. b. nevadensis*).

^f Pairwise comparison between three subspecies of the Sage Sparrow and two subspecies of the Black-throated Sparrow (*A. b. deserticola*, *A. b. opuntia*).

Nucleotide divergence between the two subspecies of Black-throated Sparrow (Genotypes 5 and 6) was greater than that found among subspecies of the Sage Sparrow, in keeping with their greater geographic separation. Five variable sites were detected (Table 2), all of which were silent sites in the third position of the codon. Four of these changes were transitions and one was a tranversion (Table 3).

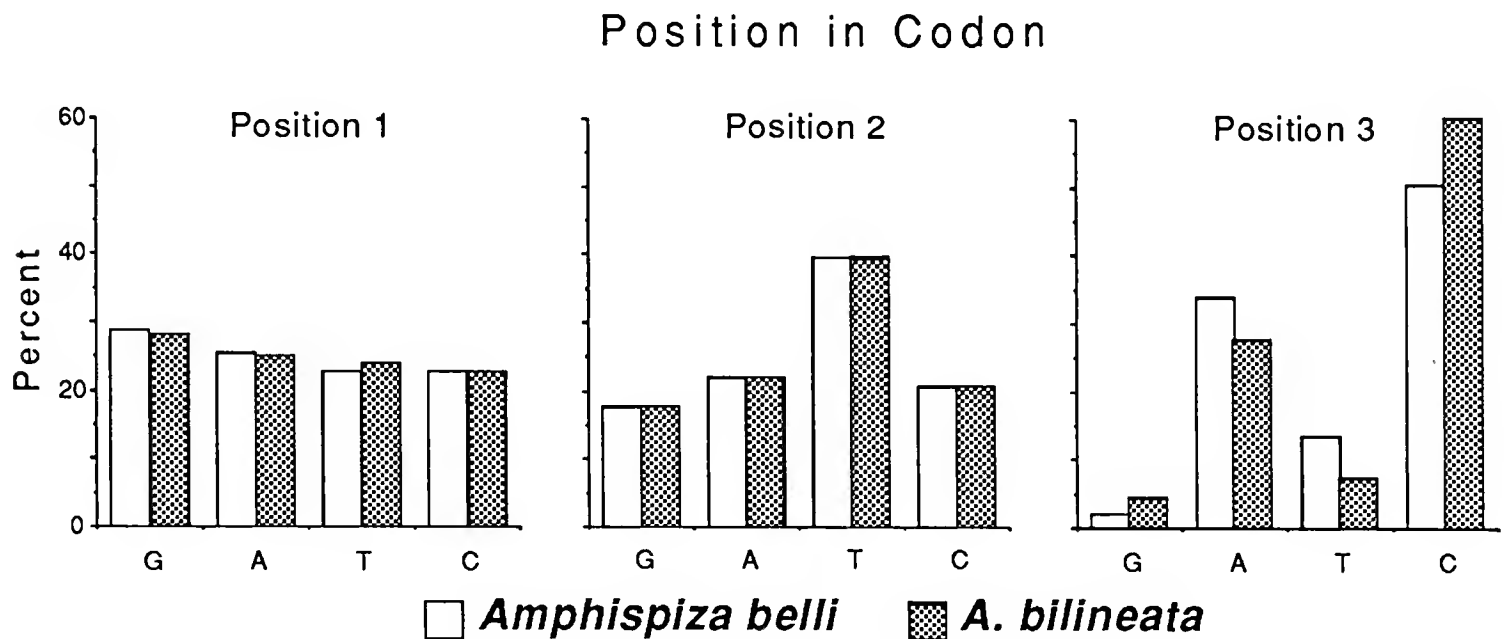


FIGURE 2 - Average percent base composition of 1st, 2nd, and 3rd positions in codons for 12 cytochrome b sequences of the Sage Sparrow and two sequences of the Black-throated Sparrow. A total of 96 codons (288 nucleotides) was examined for all 14 sequences.

INTERSPECIFIC MTDNA VARIATION. In contrast to the weak degree of intraspecific divergence, base sequences of the Sage Sparrow and Black-throated Sparrow showed numerous differences. Sequences of the two species varied at 35 sites (Table 2), 27 of which were silent. Transitions predominated over transversions, with 25 transitions and six-seven transversions occurring between pairs of individuals representing the species (Table 3). Of the 35 variable sites, seven (4 transitions, 3 transversions) were in the first position of the codon, one (transition) was in the second position, and 27 (23 transitions, 4 transversions) were in the third position. Finally, we noted the insertion of a guanine between the 64th and 65th codons in the Black-throated Sparrow that was lacking in the Sage Sparrow.

Relationship between nucleotide variation and taxonomic level

Percentage mtDNA sequence divergence increased with taxonomic level (Table 4). Pairs of individuals or taxa in the genus *Amphisipiza* differed from 0.1% (intrapopulation) to 10.9% (interspecific congeners). Interfamilial comparisons between *Amphisipiza* (Emberizidae) and *Corcorax* (Grallinidae) or *Pomatostomas* (Muscicapidae) (Kocher et al. 1989) yielded an average percent nucleotide difference of 13.9% to 17.4%, respectively. In interordinal comparisons between *Amphisipiza* (Passeriformes) and *Gallus* (Galliformes) (Desjardins & Morais 1990), the average percent nucleotide difference was 19.7%.

The ratio of transitions to transversions showed a corresponding trend with taxonomic level (Table 4). A bias toward transitions prevailed in all comparisons of sequence divergence within *Amphisipiza*. At the interfamilial level, approximately equal numbers of transitions and transversions accounted for the differences among taxa. Transversions outweighed transitions when comparing sequences between orders.

Percent base composition of sequences of *Amphispiza*

The percent base composition of codons, by position, is presented in Figure 2 for the 12 Sage Sparrow sequences and the two Black-throated Sparrow sequences. The four nucleotides occurred in approximately equal proportions in first position sites in both species. Second position sites were biased toward thymine (39.6%), with no difference in the percent base composition of second positions between the Sage Sparrow and Black-throated Sparrow. A stronger compositional bias was observed in third position sites, where both guanine (2.1-4.5%) and thymine (7.3-13.5%) occurred in low percentages relative to adenine (27.8-33.9%) and cytosine (50.5-60.4%). The bias against guanine at third position sites is a general feature of vertebrate mtDNA (Kocher et al. 1989). However, the deficiency of thymine at the same position appears to be an unusual characteristic of avian mtDNA (Kocher et al. 1989).

DISCUSSION

Nucleotide sequence difference versus allozymic divergence

Johnson & Marten (in prep.) surveyed electrophoretic variation within and among 24 populations of the Sage Sparrows and Black-throated Sparrow, including the 8 populations analysed in the present study. Nei's (1978) genetic distances within subspecies of the Sage Sparrow were 0.001 for Beegum versus Castaic (*A. b. belli*), 0.005 between Panoche Hills and Chalfant Valley (*A. b. canescens*), and 0.000 between Rattlesnake Flat and Plush (*A. b. nevadensis*). Electrophoretically, the population from Chalfant Valley was essentially identical to populations from both Rattlesnake Flat ($D = .001$) and Plush ($D = .000$), indicating a closer affinity to *A. b. nevadensis* than to *A. b. canescens* (Johnson & Marten in prep.). The data on nucleotide sequence divergence in cytochrome b support the conclusion from the allozyme analysis that Sage Sparrows from the northern Owens Valley are best placed with *A. b. nevadensis*. Based on the same subset of populations (excluding Chalfant Valley), average Nei's D values between subspecies of the Sage Sparrow were 0.0005 for *A. b. belli* versus *A. b. canescens*, 0.0105 between *A. b. belli* and *A. b. nevadensis*, and 0.0075 between *A. b. canescens* and *A. b. nevadensis*. Both the allozyme and mtDNA data clearly indicate that *A. b. belli* is more closely allied to *A. b. canescens* than either is to *A. b. nevadensis*.

Quantitative comparisons of electrophoretic variability with mtDNA sequence divergence offer insight into evolutionary relationships. Thus, we calculated the average pairwise nucleotide difference between populations (= number of transitions + transversions [from Table 3] divided by the number of comparisons in each set of populations) and computed a simple correlation coefficient (r) between each of those values and the corresponding value for Nei's D . The correlation between the two matrices was impressively high ($r = 0.984$), suggesting that both techniques provided a robust estimate of the actual amount of genetic difference present in *Amphispiza*. When the same two matrices were subjected to a Mantel test, $t = 3.9908$ and $P < .001$, similarly indicating a highly significant association.

Utility of mtDNA base sequence analysis for assessing relationships at different taxonomic levels

Despite fundamental changes in the organization of the avian mtDNA genome (Desjardins & Morais 1990), birds, like mammals (Bibb et al. 1981, Wilson et al. 1985,

Howell 1989), show differences in the inherent variability of regions within and between genes in the mtDNA (Kocher et al. 1989). Such variation would profoundly influence the relative utility of different portions of the mtDNA for phylogenetic analysis at various taxonomic levels. Kocher et al. (1989) demonstrated the usefulness of cytochrome b for the study of evolutionary relationships at the species level and above. For intraspecific studies, however, less conserved areas of mtDNA, such as the displacement-loop (control) region (Bibb et al. 1981, Wilson et al. 1985), might offer better information for assessing genetic divergence within and between populations. Nonetheless, the strong concordance between patterns of variation in allozymes and cytochrome b within *Amphispiza* suggests that cytochrome b sequences, at least in the region chosen here, can be useful for assessing relationships in this group down to and including populations (Wilson et al. 1985). The degree to which cytochrome b sequences might elucidate intraspecific relationships in other avian taxa remains to be studied.

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MICROCOMPLEMENT FIXATION: PRELIMINARY RESULTS FROM THE AUSTRALASIAN AVIFAUNA

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ABSTRACT. Microcomplement fixation is being used to test conflicting phylogenetic hypotheses relevant to the evolution of various groups of Australasian birds. The studies are as yet incomplete, but preliminary results suggest that: 1) Albumin immunologic evolution in the Zebra Finch *Taeniopygia guttata* has been far from clock-like. 2) The Australian passerines are indeed a monophyletic assemblage, as indicated by DNA/DNA hybridisation, but the timing of the origin of this group remains inconclusive. 3) Albumin evolution in the parrots (Psittaciformes) has either been relatively slow, or the parrots are not a Gondwanan group. 4) The Australian Honeyeater (Meliphagid) radiation is monophyletic with respect to *Melilestes* and *Myzomela*. 5) The Australian chats *Ephthianura* and the Gibber Bird *Ashbyia* are sister taxa having close affinity with the Australian meliphagids. 6) The Australian "mudnesters" are not monophyletic, the Mudlark *Grallina* being a monarch flycatcher, closely allied to *Myiagra*. 7) The Australian treecreepers *Climacteris* are a monophyletic group that includes *Cormobates leucophea*, and that has affinities with the Meliphagidae.

Keywords: Albumin, microcomplement fixation, passerines, parrots, finches, treecreepers, chats, mudnesters, honeyeaters.

INTRODUCTION

Microcomplement fixation is a quantitative immunological procedure used for estimating the number of amino acid substitution differences between homologous proteins (Wilson et al. 1977). It has been used extensively to probe evolutionary relationships among taxa, mainly in the higher vertebrates (e.g. Sarich 1969, Maxson et al. 1982, 1988).

For some proteins, the procedure has revealed a high level of rate uniformity within many vertebrate groups, and hence has been used as a molecular dating device (e.g. Sarich 1969, Maxson et al. 1982). Moreover, these studies have suggested that, in general, most vertebrates seem to have similar rates of molecular evolution for a given protein (e.g. Maxson et al. 1975). A possible exception is birds. Microcomplement fixation studies using mainly albumin and transferrin have been interpreted as indicating a slower rate of protein evolution in birds (Prager et al. 1974), a view supported by DNA/DNA hybridisation studies (Sibley & Ahlquist 1986). However, this view has not received unanimous support (e.g. Wilson 1988).

Over the past several years, a group of us have been using microcomplement fixation of albumin and to a lesser extent transferrin to probe evolutionary problems in the Australian avifauna. These studies are as yet incomplete, but this symposium provides an opportunity for us to present preliminary data that are relevant not only to the

origins and evolution of the Australian avifauna, but also to our understanding of protein immunologic evolution in birds. Because detailed analyses will be presented elsewhere, we simply present herein representative data that illustrate the approach.

METHODS

The microcomplement fixation procedure used follows closely that described by Champion et al. (1974) and Maxson & Maxson (1990). Antisera were raised in rabbits (three per antigen) over a period of three months, and the purity of antisera checked by immunoelectrophoresis. All results are expressed as immunological distances - ID (Champion et al. 1974).

RESULTS AND DISCUSSION

Unequal rates of albumin immunologic evolution

As part of a study of molecular relationships among finches of the subfamily Estrildinae, we discovered an unusual case of rapid albumin immunologic evolution in the Zebra Finch, *Taeniopygia guttata* (Baverstock et al. 1990a). A sample of the relevant data is shown in Table 1. Within the Estrildinae, *Neochmia* and *Taeniopygia* are members of the grassfinch tribe Estrildini, and *Lonchura* of the tribe Lonchurini, whereas *Passer* is a member of a related subfamily Passerinae, sparrows. Antiserum to *Neochmia temporalis* albumin recognises the close similarity of albumin of Double-barred Finch *T. bichenovii* (ID = 3) and of *Lonchura* (ID = 2), but the albumin of *T. guttata* is immunologically quite distinct, with an ID of 38, exceeding that of *Passer domesticus* (ID = 24). Antiserum to albumin of *T. guttata* gives a similar reciprocal response, with IDs of 32 to 39 to other estrildines including its congener *T. bichenovii*.

There are two possible explanations for these results: either the taxonomy of *T. guttata* at the generic, tribal and subfamilial level is in error, or the albumin of *T. guttata* has undergone a rapid immunological change. Chromosomal and allozymic data (Christidis 1986a,b, 1987a,b) indicate the latter. Indeed, microcomplement fixation studies of transferrin, a protein that typically evolves at about twice the rate of albumin (Prager et al. 1974), yielded the expected result, with *T. bichenovii* closest to *T. guttata* (Table 1).

Whatever the explanation for the dramatic change in the immunological properties of *T. guttata* albumin (Baverstock et al. 1990), the data clearly indicate that rates of albumin immunologic evolution are not always uniform among lineages of birds.

Monophyly of the Australian passerine radiation

Based upon DNA/DNA hybridisation studies, Sibley & Ahlquist (1985) concluded that many Australian passerine groups had been incorrectly placed among northern hemisphere-centred families, and that they in fact represented an endemic radiation within Australia (Parvorder Corvi). They further suggested that this group had a Gondwanan origin which, based on a DNA/DNA molecular clock, separated from the Parvorder Muscicapae (= Passerida) 55 to 60 mya.

TABLE 1 - Immunological distances (IDs) of selected finches to rabbit anti-albumin of *Neochmia temporalis*(*Nt*), *Taeniopygia guttata* (*Tg*) and *Lonchura oryzivora* (*Lo*) and to rabbit anti-transferrin of *T. guttata*.

Antigen	Antibody				
	Anti-albumin		<i>Lo</i>	Anti-transferrin	
	<i>Nt</i>	<i>Tg</i>		<i>Pd</i>	<i>Tg</i>
<i>Neochmia temporalis</i> (<i>Nt</i>)	0	39	5	23	12
<i>Taeniopygia guttata</i> (<i>Tg</i>)	38	0	31	52	0
<i>Lonchura oryzivora</i> (<i>Lo</i>)	2	33	0	26	14
<i>Passer domesticus</i> (<i>Pd</i>)	24	52	22	0	17
<i>Neochmia ruficauda</i>	2	32	-	-	9
<i>Taeniopvgia bichenovii</i>	3	34	-	-	9

We have tested these conclusions with microcomplement fixation of albumin. Our data (Table 2) are consistent with the hypothesis that the Parvorder Corvi of Sibley and Ahlquist (1985) is a monophyletic assemblage. Moreover the data are, with few exceptions, consistent with the branching relationships they proposed among the families.

The timing of the separation of the Parvorders Corvi and Passerida by albumin immunology is more problematic. The relationship $T = 0.6 D$ (where T = time in millions of years and D = albumin ID) has been used extensively for the "albumin clock" (e.g. Wilson et al. 1977), but Sarich (1985) has since suggested that the relationship $T = 0.35 D$ is more appropriate for the placental mammal orders. The relationship between T and D for birds is even more controversial. Initial results (e.g Prager et al. 1974) led to the conclusion that in birds the rate of albumin evolution, and indeed of the total genome (Sibley & Ahlquist 1986), was about half that of other vertebrates, although Wilson (1988) has subsequently questioned the calibration of these clocks.

Our data have corroborated the findings of Prager et al. (1974) that albumin IDs between the orders of birds are about 40 to 50. If the orders of birds were already present in the late Cretaceous (Olsen 1985, Feduccia 1980), then this is a clear indication of a slower rate of albumin evolution in birds than in other vertebrates by about one half. Applying a formula of $T = 1.2 D$ to the passeriform data, we obtain a divergence time between the Parvorders Corvi and Passerida of about 50 mya. Such a timing is compatible with a Gondwanan origin for the Parvorder Corvi, in accordance with the proposal of Sibley & Ahlquist (1985). Applying the more usual formula gives a separation time of about 25 mya, which is too short for a Gondwanan origin.

Albumin evolution in the parrots (Psittaciformes)

The order Psittaciformes presently occurs in Australia and New Guinea, New Zealand, South America, Africa, India and Southeast Asia, precisely the distribution expected of a Gondwanan group (Smith 1975), notwithstanding a meagre European fossil record in the Tertiary. We therefore undertook an albumin immunologic study of this group in the hope of shedding further light on rates of molecular evolution in birds. A representative set of results is shown in Table 3.

TABLE 2 - Immunological distances of selected Passeriforms to rabbit anti-albumin of the honeyeater *Anthochaera carinata* (Ac), the chat *Ephthianura tricolor* (Et), and the treecreeper *Climacteris picumnus* (Cp). Classification follows Sibley and Ahlquist (1985).

	Ac	Et	Pc
Parvorder Corvi			
Meliphagidae			
<i>Anthochaera paradoxa</i>	0	13	16
<i>Anthochaera chrysoptera</i>	0	-	-
<i>Acanthagenys rufogularis</i>	0	-	-
<i>Phylidonyris novaehollandiae</i>	6	9	21
<i>Lichenostomus penicillata</i>	4	13	14
<i>Acanthorhynchus tenuirostris</i>	2	-	-
<i>Certhionyx variegatus</i>	8	-	27
<i>Myzomela sanguinolenta</i>	21	18	38
<i>Melilestes megarhynchus</i>	26	16	35
Ephthianuridae			
<i>Epthianura tricolor</i>	22	0	18
<i>Epthianura albifrons</i>	-	3	-
<i>Epthianura aurifrons</i>	-	2	-
<i>Ashbyia lovensis</i>	-	2	-
Acanthizidae			
<i>Pardalotus striatus</i>	15	17	18
<i>Acanthiza chrysorrhoa</i>	26	36	32
Maluridae			
<i>Malurus pulcherrimus</i>	16	20	17
Corvoidea			
<i>Corcorax melanorhamphos</i>	27	42	15
<i>Grallina cyanoleuca</i>	22	21	24
Menuroidea			
<i>Menura novaehollandiae</i>	21	-	23
<i>Climacteris picumnus</i>	23	27	0
<i>Climacteris affinis</i>	-	-	7
<i>Climacteris erythrops</i>	-	-	7
<i>Climacteris leucophaea</i>	-	-	10
Parvorder Passeri			
Turdidae			
<i>Turdus merula</i>	39	-	33
Hirundinidae			
<i>Hirundo neoxena</i>	33	-	31
Passeridae			
<i>Passer domesticus</i>	41	45	36
Zosteropidae			
<i>Zosterops lateralis</i>	47	43	34
Alaudidae			
<i>Anthus novaeseelandiae</i>	55	40	36

The immunological distances are again compatible with a slow rate of albumin evolution in birds if the parrots are indeed Gondwanan in origin. The phylogenetic picture revealed by these data is as compatible with a vicariant Gondwanan origin as with dispersal from Eurasia. If dispersal were the prime mechanism underlying the distribution of parrots, we might expect Indian parrots to be more closely related to

TABLE 3 - Immunological distances of selected parrots (Psittaciformes) to rabbit anti-albumin of the Bluebonnet *Northiella haematogaster* (*Nh*), the Budgerigar *Melopsittacus undulatus* (*Mu*), the Indian Ringneck *Psittacula krameri* (*Pk*), and the Peachface Lovebird *Agapornis roseicollis* (*Ar*).

Antigen	Antibody			
	<i>Nh</i>	<i>Mu</i>	<i>Pk</i>	<i>Ar</i>
<i>Northiella haematogaster</i> (Aust)	0	20	9	27
<i>Melopsittacus undulatus</i> (Aust)	20	0	15	33
<i>Psittacula krameri</i> (India)	9	15	0	26
<i>Agapornis roseicollis</i> (Africa)	27	33	26	0
Australia				
<i>Glossopsitta concina</i>	3	14	10	37
<i>Cacatua roseicapilla</i>	7	18	13	28
New Zealand				
<i>Strigops habroptilus</i>	16	29	17	29
<i>Nestor meridionalis</i>	8	24	16	28
<i>Cyanorhamphus novaezealandiae</i>	9	16	8	25
India				
<i>Psittacula alexandriae</i>	9	15	0	27
America				
<i>Deroptyus accipitrinus</i>	4	16	7	27
<i>Ara ararauna</i>	8	20	9	26
<i>Pyrrhura picta</i>	9	-	13	26
<i>Rhynchopsitta pachyrhyncha</i>	5	19	9	26
Africa				
<i>Psittacus erithacus</i>	14	20	14	27
<i>Poicephalus meyeri</i>	13	29	12	30

Australian or to African parrots than to the parrots of South America and New Zealand. Yet there is no evidence for either in the data.

A curious result is the highly divergent albumin of the Budgerigar *Melopsittacus undulatus* from the other Australian parrots. Outgroup analysis revealed that here, as in the Zebra Finch, the high divergence is due to rapid evolution of the immunologic properties of Budgerigar albumin. Interestingly the albumin of *Agapornis roseicollis* is also highly divergent from the other African parrots compared. We were unable to determine the basis for this divergence.

Relationships within the honeyeaters Meliphagidae

Our protein data (Table 2) show that the New Guinean-centred genera *Myzomela* and *Melilestes* fall well outside other meliphagids represented, or that their albumins have had unusually fast rates of albumin evolution. DNA/DNA hybridisation data (Sibley & Ahlquist 1985) also suggest that these genera were distantly related to each other and to other meliphagids.

Relationships of the Australian chats Ephthianuridae

Two genera are typically included in the Ephthianuridae, *Ephthianura* and *Ashbyia*. They have usually been considered monophyletic, although *Ashbyia* has at times

been associated with the pipits (Motacillidae). The affinities of the family have been considered to lie with the Australian warblers, although aspects of morphology (Parker 1973) and DNA/DNA hybridisation (Sibley & Ahlquist 1985) place it with the Meliphagidae.

Our data (Table 2) unequivocally align *Ashbyia* with *Ephthianura*, and they are consistent with monophyletic links with the Meliphagidae.

The relationships of the Australian mud-nesters

The Australian mud-nesters have traditionally included the Magpielark *Grallina cyanoleuca*, the Apostle bird *Struthidea cinerea*, and the White-winged Chough *Corcorax melanorhamphos*. A fourth species, the Torrent-lark *Grallina bruijni*, occurs in Papua New Guinea. The three genera have variously been combined in the same family, split into three separate families, or *Struthidea* and *Corcorax* have been grouped in one family and *Grallina* in another. More recently, DNA/DNA hybridisation studies have corroborated the last arrangement, indicating that *Grallina* is not related to the other two mudnesters but to the monarchine flycatchers, notably *Monarcha* and *Myiagra* (Sibley & Ahlquist 1985). Relevant microcomplement fixation data (Table 4) are unequivocal with regard to *Grallina*, clearly aligning it with the monarchine, *Myiagra*.

TABLE 4 - Immunological distances of selected Corvoidea to rabbit anti-albumin of the Mudlark *Grallina cyanoleuca*.

Grallinidae	
<i>Grallina cyanoleuca</i>	0
<i>Grallina bruijni</i>	0
Corcoracidae	
<i>Corcorax melanorhamphus</i>	29
<i>Struthidea cinerea</i>	20
Monarchidae	
<i>Myiagra</i> (average 4 spp.)	2
<i>Monarcha</i> (average 6 spp.)	8
<i>Rhipidura</i> (average 5 spp.)	10
Corvidae	
<i>Corvus bennetti</i>	22
Cracticidae	
<i>Gymnorhina tibicen</i>	24

The relationships of the Australian Treecreepers, family Climacteridae

The Australian treecreepers have been variously aligned with holarctic creepers Certhiidae (Gadow 1883), with the honeyeaters Meliphagidae (Harrison 1969, Parker 1982), as an Australo-Papuan group with no close affinities (Schodde 1975, Orenstein 1977, Ames 1987), or distantly related to the lyrebirds *Menura* and bowerbirds Ptilonorhynchidae (Sibley & Ahlquist 1985). Moreover, Parker (1982) suggested that the *C. leucophaea* superspecies was sufficiently distinct from other climacterids as to be paraphyletic with an independent meliphagid ancestry.

Albumin data (Table 2) are consistent with *Climacteris sensu lato* being a monophyletic unit, in which *leucophaea* nevertheless lies outside the other three species. There is no evidence for an especially close relationship of *Climacteris* to any

other group; the closest group appears to be the Meliphagidae, but the Menuridae are well distant.

The future

Much of the speculation presented herein is based upon one-way immunological reactions and therefore must be treated with caution, especially in view of the indications of grossly unequal rates of albumin evolution in the Zebra Finch. Nevertheless one-way reactions are useful for distinguishing markedly different phylogenetic hypotheses, and for highlighting taxonomic problems warranting additional investigation.

There is no doubt that recent developments in molecular technology are bringing nucleic acid sequencing into the realm of phylogenetic hypothesis testing as a practical method. It is apparent that sequence data are far superior to immunological techniques such as microcomplement fixation for phylogenetic analysis.

Nevertheless, information from microcomplement fixation data has given a wealth of background information on phylogenetic relationships among higher vertebrates, and provided the basis for considerable debate regarding rates of molecular evolution, times of phylogenetic divergence, and modes and tempos of morphological, behavioural and chromosomal evolution.

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AVIAN SYSTEMATICS BY SEQUENCE ANALYSIS OF mtDNA

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ABSTRACT. Sequence data are qualitatively different from other DNA data in giving precise knowledge of the nature of genetic differences. This facilitates a functional analysis and differential weighting of characters based on empirical knowledge of the mode of evolution of the particular gene and of more general molecular constraints. The main disadvantage is that for practical reasons only minute parts of a genome can be sequenced. The power of resolution and the limitations for DNA sequence analysis are discussed and exemplified by 42 sequences of 287 base pairs (bp) in the cytochrome-b (cyt-b) gene of mitochondrial DNA (mtDNA) from 30 different bird species covering a wide taxonomic range. Resolving power is good at the species level, roughly within 1 - 30 million years since a common ancestor (mya). However, the 287 bp are insufficient when analyzing more closely related forms, e.g. intra-specific relations, as well as more distant relationships. To resolve relationships at these distances, DNA fragments more variable than cyt-b and/or longer stretches of DNA have to be sequenced. Because of very slow rates of amino-acid replacing substitutions, phylogenetic information is retained even over 600 mya.

Keywords: Avian systematics, mitochondrial DNA, DNA sequence analysis, polymerase chain reaction, sequence evolution.

INTRODUCTION

Comparative morphology and anatomy have been the main tools for reconstructing avian evolution. Difficulties arise for this approach when dealing with very close relatives because of few characters, and on all systematic levels because of the difficulties in discovering convergence and parallelism. Overcoming these hurdles is the primary reason for the interest in molecular data and especially DNA, which promises to provide informative, comparable and 'objective' data.

There are currently three, quite different, DNA techniques in use: DNA/DNA hybridization, which aims to compare whole genomes; restriction fragment length polymorphism analysis (RFLP), scoring part of the substitutions in a small fragment of the DNA; and sequencing analysis, revealing the actual genetic code of a DNA fragment. In the following I will concentrate on DNA sequence analysis (for survey see Arctander & Fjeldsa in press, Sibley & Ahlquist 1986, Quinn & White 1987).

Technical achievements in biotechnology, such as the development of the polymerase chain reaction (PCR), have made it feasible to sequence homologous DNA segments from a wide variety of organisms. Sequence data differ qualitatively from other DNA data, giving precise knowledge of the nature of genetic differences. This facilitates a functional analysis and differential weighting of characters based on empirical knowledge of the mode of evolution of the particular gene and of the existence of molecular constraints. The DNA sequence data illustrate principles of molecular evolution and, therefore, clarify the relationship between phenotypic and molecular evolution. Sequence data are superior in these ways and, therefore, highly desirable. The main

disadvantage is that for practical reasons only minute fragments of the genome can be sequenced.

The present paper addresses the question: Can a few hundred base pairs provide reliable historical information? And if so, what is the power of resolution and what are the limitations of this approach? The data analyzed are all from mitochondrial DNA (mtDNA), but except for one case (*Laniarius*) nuclear DNA could as well have been analyzed. A more detailed presentation and discussion of the data will appear elsewhere.

THE POWER OF RESOLUTION AT DIFFERENT SYSTEMATIC LEVELS

Resolution at the species level

Clear demarcation of species can be difficult, especially when dealing with allopatric populations. The biological species definition is operatively unhandy (McKittrick & Zink 1988, Haffer 1986). Species limits are often ambiguous because traditional methods provide few characters, and because analysis can be hampered by subjective characterization; concealed parallelism and convergence, especially when most characters are in terms of color hues, body size, and so on, also confound analysis. The following two examples illustrate the potential of DNA sequence data at this level.

A NEW SPECIES OF LANIARIUS? Last year in Bulu Burti, Somalia, a Boubou *Laniarius* was captured (Smith et al. in press). From morphology, it was judged to be a new species but in spite of months of observations only this individual was recorded. This naturally raises the question: Could it be a rare result of a hybridization or a color freak? These questions can be answered by analysis of mtDNA. MtDNA is maternally inherited so any hybrid or morph will have the mtDNA from the mother species. Comparing mtDNA from this individual with species that could possibly have provided the mother should resolve the question.

Another advantage of DNA analysis is that small amounts of tissue (blood or feather pulp; Arctander 1988, Arctander & Fjeldsa in press) are needed for analysis, and collection of this rare bird was unnecessary.

A 295 base pair (bp) fragment of the mtDNA cytochrome b (cyt-b) gene was sequenced from 6 different *Laniarius* species and one *Telophorus* (outgroup). This data set contains 65 variable sites of which 44 are phylogenetically informative.

DNA sequence cannot determine species status in its strict biological sense. However, in this case we concluded that the mother of the Bulu Burti Boubou did not come from any of the examined species, ruling out hybridization and color morphism. The number of substitutions in pairwise comparisons including this taxon (average transversions 4.5, transitions 22.4 [transversion: purine to pyrimidine, or vice versa; transition: purine to purine or pyrimidine to pyrimidine]) corresponds well with the amount of variation observed within the other examined *Laniarius*, which are all considered good species (mean transversions 4.3, transitions 23). Only three substitutions (two transitions and one transversion, all silent) were found between the two *L. luhderi* populations 400 km apart from Sudan and from Kenya, respectively. Only one replacement substitution was observed in the whole data set.

TABLE 1 – Species analysed, the source of DNA and status of publication. Refers to the number of sequences from different individuals of the particular species. DNA was obtained from several different sources, blood samples collected and preserved according to Arctander (1988), blood quills from alcohol-preserved feathers (Smith et al. in press), muscle tissue first frozen, later alcohol-preserved (e.g. Edwards et al. in press) and from small fragments of old museum skins (e.g. Smith et al. in press, Paabo 1989). DNA was extracted following standard methods (Arctander 1988, Smith et al. in press). A 287 bp fragment of the mtDNA cyt-b gene spanning 95 amino acids was analyzed for all species in this study. They cover the positions 14842 to 15128 (enumerated according to the corresponding human sequence, Anderson et al. 1981). The *Gallus*, *Bos*, *Xenopus* and *Paracentrotus* sequences are taken from the literature. Prior to sequencing of all the other species the DNA was amplified via the polymerase chain reaction (PCR) (Erlich 1989, Saiki et al. 1988). Double stranded amplifications were followed by single stranded ones, whereby sufficient copies of the desired DNA fragment were obtained for dideoxy termination sequencing (Sanger 1977, Gyllenstein & Erlich 1988). The Primers HL14841 and HH15149 (Kocher et al. 1989) were used for the amplifications, which were performed in 50 µl reactions running 30-35 cycles, and with a 1:100 dilution of one primer in the single-stranded reaction. For the phylogenetic analysis the PHYLIP 3.3 programs DNAPARS, DNABOOT and DNAML (Felsenstein 1990) and CMP (Siegismund, unpublished) were used.

Samples		No.DNA source	Publication
1	<i>Laniarius</i> , unnamed	1 feather	Smith et al. in press
2	<i>L. aethiopicus</i>	1 skin	
3	<i>L. turatii</i>	1 blood	
4-6	<i>L. luhderi</i>	3 skin	
7	<i>L. ruficeps</i>	1 skin	Edwards et al. in press
8	<i>L. barbarus</i>	1 blood	
9	<i>Pomatostomus temporalis</i>	1 tissue	
10	<i>P. ruficeps</i>	1 tissue	
11	<i>P. isidori</i>	1 tissue	unpublished
12-17	<i>Scytalopus magellanicus ssp.</i>	6 blood/tissue	
18-20	<i>S. unicolor</i>	3 blood	
21-22	<i>S. femoralis</i>	2 blood	
23	<i>S. latebricola</i>	1 blood	Edwards et al. in press
24-26	<i>S. unnamed</i>	3 blood/tissue	
27	<i>Melanoparaia maximiliani</i>	1 blood	
28	<i>Grallaria andicola</i>	1 blood	
29	<i>Ampelion stresemanni</i>	1 blood	unpublished
30	<i>A. rubrocristatus</i>	1 blood	
31	<i>Phytotoma rutila</i>	1 blood	
32	<i>Pireola arcuata</i>	1 blood	
33	<i>Pipra coronata</i>	1 skin	Edwards et al. in press
34	<i>Myiarcus tuberculifer</i>	1 blood	
35	<i>Elaenia pallatangae</i>	1 blood	
36	<i>Pachyramphus validus</i>	1 skin	
37	<i>Mionectes striaticollis</i>	1 blood	unpublished
38	<i>Asthenes dorbignyi</i>	1 blood	
39	<i>Pitta sordida</i>	1 blood	
40	<i>Catharus guttatus</i>	1 blood	
41	<i>Alca torda</i>	1 blood	Desjardins & Morais 1990
42	<i>Gallus gallus</i>	1	
43	<i>Bos taurus</i>	1	Anderson et al. 1982
44	<i>Xenopus laevis</i>	1	Roe et al. 1985
45	<i>Paracentrotus lividus</i>	1	Cantatore et al. 1989

In the light of the DNA analysis the Bulo Burti Boubou is as genetically distinct as any of the other examined *Laniarius* species. Apart from answering our primary question the analysis places the new bird in the phylogeny of the *Laniarius*. The topology of the resulting phylogeny was in good agreement with conclusions based on morphology.

SCYTALOPUS,. MORPHOLOGICALLY INDISTINGUISHABLE. Tapaculos of the genus *Scytalopus* are small, short-tailed, blackish sedentary suboscines widespread in the Andes and in southeastern Brazil. The currently accepted taxa are extremely difficult to distinguish morphologically. Observation that the songs and male responses to play-back were strongly differentiated (N. Krabbe pers. com., Fjeldsa & Krabbe 1990) revealed that the number of biological species probably has been underestimated.

Comparisons based on the 287 bp's covering the same gene fragment of mtDNA cyt-b as used for *Laniarius* show approximately the same numbers of transitions and transversions as for *Laniarius* (mean transitions 26, transversions 4.4,see Table 2). Sequencing several individuals originating from the same geographic region in all cases except one revealed no differences (the one individual was out of a group of 10 and had two silent 3rd position transitions). Once again, the sequence data do not automatically define these taxa as good biological species, but show that many allopatric forms that scarcely differ morphologically, but do so vocally, are clearly distinguishable when analyzing DNA, and are as distinct as morphologically very separate *Laniarius* species, for example. These preliminary results indicate that several small isolated populations should be ranked as species and that a complete revision of the group probably is necessary.

These *Laniarius* and *Scytalopus* sequences support taxonomic conclusions at the within-genus level.

TABLE 2 – Transitions, transversions and amino acid replacements at different systematic levels.

cyt-b 287 bp	Transitions			Transversions			Replacements			
	Range	Mean	%	Range	Mean	%	Range	Mean	%	N
Bush shrikes	15-28	22	7.7	2-7	4.1	1.4	0-1	0.1	0.1	6
Austr. babblers ¹	23-33	29	10.1	1-7	4.6	1.6	0-7	4.7	4.9	3
Tapaculos	8-40	26	9.1	1-11	4.4	1.5	0-2	0.2	0.2	15
Cotingas	37	37	12.9	12	12.0	4.2	5	5	5.3	2
Intra specific	0-3	0.3	0.0	0-1	0.1	0.0	0	0	0	19 ²
Intra genus	8-40	23.2	8.1	1-12	4.5	1.6	0-7	0.3	0.4	26 ³
Inter family	22-44	29.6	10.3	14-33	27.9	9.7	2-9	5.5	5.8	8 ⁴
Higher taxa	19-29	24.6	8.6	11-28	22.0	7.7	4-9	6.7	7.1	5 ⁵
To Cow	19-33	27.5	9.6	42-58	50.0	17.4	20-23	21.2	22.6	1 ⁶

¹ The relatively high number of substitutions are almost entirely due to *Pomatostomus isidori*.
² Substitutions were only detected between two of the 19 individuals.
³ Representing four genera with 2, 3, 6 and 15 species respectively; see first part of the table.
⁴ The following sub-families and families are compared: Cotinginae, Piprinae, Tityrinae, Tyranninae, Mionectidae, Furanidae, Rhinocryptidae and Formicaridae.
⁵ Single species from the following higher categories: Tyrannides, Eurylamides, Passeres, Picae and Charidriformes.
⁶ One Cow compared to the species listed in note ⁵

Resolution at the family level

PHYTOTOMA - OWN FAMILY? *Phytotoma*, the plantcutters, were previously placed in a monotypic family because of their conspicuously serrated mandibular edges and syringeal structure (e.g. Warter 1965 [cited in Lanyon & Lanyon 1989], Ames 1971). Sibley and Ahlquist (1985) placed *Phytotoma* within the Cotinginae but did not include them in their DNA analysis, whereas Lanyon and Lanyon (1989) retain the family Phytotomidae.

Using either the principle of maximum parsimony or maximum likelihood (Felsenstein 1990), a genealogical tree based on 287 bp of cyt-b from the mtDNA of 12 different Tyrannides (and a *Pitta* included as outgroup; Table 1: 12, 28-39) clearly places *Phytotomas* within the Cotinga family, near the genus *Ampelion*.

The data show a varying degree of resolving power concerning the other groups of the Tyranni. The Funarii represented by *Asthenes*, *Scytalopus* and *Grallaria* is very well supported as a monophyletic group. Other deeper nodes are not nearly as well resolved, indicating insufficient phylogenetic information probably due to back-mutations in positions that are relatively free to vary. The basic radiation of these groups might have happened over a very short period of time as suggested by Sibley and Ahlquist's data (1988), which would make the resolution of these nodes difficult.

Resolution at the level of the basal radiation of an order

OSCINE-SUBOSCINE SPLIT; MONOPHYLY OF AUSTRALIAN OSCINES? In collaboration with S. V. Edwards and A. C. Wilson we investigated whether phylogenetic information is retained over even longer evolutionary distances. The Oscine - Suboscine dichotomy and the Sibley and Ahlquist proposed division of Passeriform birds into Passerida and Corvida (Sibley & Ahlquist 1988) were examined using 924 bp of cyt-b from 13 different Oscines and Suboscines and with a Picidae as outgroup for phylogenetic analysis. By raising the number of bp's compared to 924 even nodes as deep as the Oscine/Suboscine split can be well resolved. The resulting phylogeny has almost the same topology as that obtained by Sibley and Ahlquist using DNA/DNA hybridization, but the sequence data strongly unite Australian babblers (Pomatostomidae) and thrushes (Turdinae) and these form a sister group with Sylvioidea (*Parus*); these results contradict the monophyly of Australian oscines, Corvida, as proposed by Sibley and Ahlquist.

SEQUENCE VARIATION OVER TIME

An important reason for choosing the cyt-b gene is the apparent functional invariance of this gene mirrored in the conservative amino acid composition and pattern of variation in all studied organisms (Edwards et al. in press, Irving et al. in press, Howel 1989). The pattern of variation supports the idea that the selective pressure on this gene will not vary much between different taxa especially when closely related forms are compared. This is important because comparative analysis could be seriously flawed because of different rates of substitutions in different lineages. In the oscine/suboscine study, the suboscine branch reveals a significantly higher number of T's at third position in the reading frame than the oscine branch. This probably has nothing to do with phenotypic selection, as practically all third position substitutions are

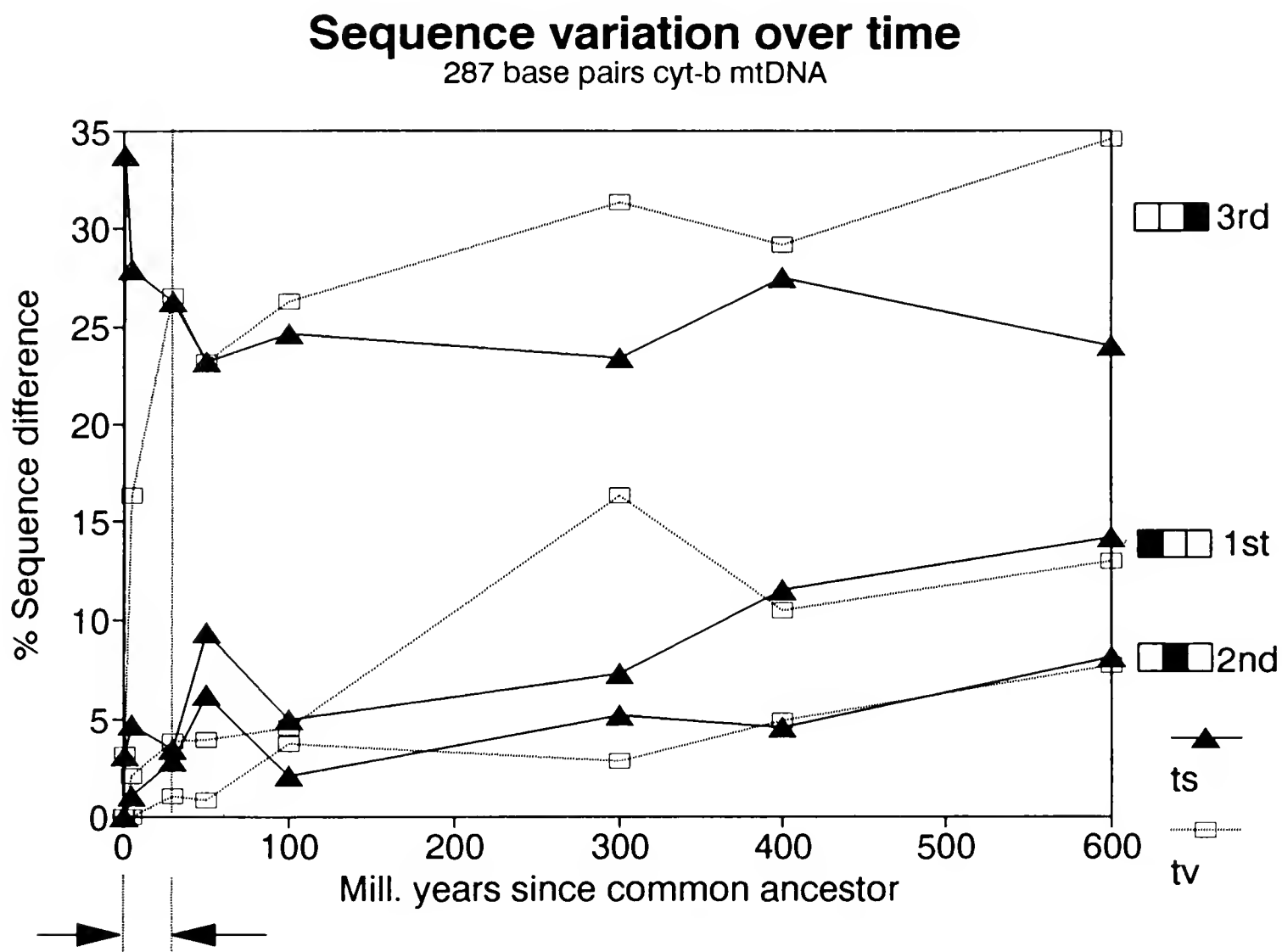


FIGURE 1 – Patterns of nucleotide substitutions spanning 600 million years for 287 base pair mtDNA cyt-b sequence for each position in the codon triplet and specified for transitions and transversions, respectively. Based on comparisons of: two *Scytalopus* (1 million years since common ancestor (mya)), their closest outgroup *Melanoparaia* (5 mya), *Ampelion* (30 mya), *Catharus* (50 mya), *Gallus* (100 mya), *Bos* (300 mya), *Xenopus* (400 mya), *Paracentrotus* (600 mya)(for references see Table 1).

silent, but is rather an example of how molecular evolutionary mechanisms can influence the pattern of substitution.

Despite its conservatism, cytochrome b of the mtDNA contains information facilitating analysis of phylogenetic relationships from the species to the ordinal level in birds. However, informative characters are few between closely related forms (e.g. only three substitutions separate *Laniarius luhderi* from Kenya and Sudan) so either very large amounts of sequence or a less evolutionary conservative region must be sequenced to study population structures, for example. This latter could for instance be the so called d-loop region of the mtDNA, which has been shown to be highly variable (Brown 1985).

The basic pattern of variation according to codon positions is as follows: 1st position: all substitutions result in amino acid replacements except C/T when the amino acid is leucine; 2nd position: all substitutions result in replacements; 3rd position: most substitutions do not result in replacements; those that do are transversions. As the amino acid sequence is very conservative few replacements occur and most variation is observed at 3rd position and for leucine also at 1st position. Over time, the variable

positions are likely to be substituted again and again ('multiple hits') destroying phylogenetic information by causing 'saturation'. All substitutions are not equally likely, and in avian mtDNA transitions seem to be about 20 times as likely as transversions at least at 3rd position (own unpublished results; S. Edwards pers. com.). Therefore, transversions will be phylogenetically informative for a much longer period of time.

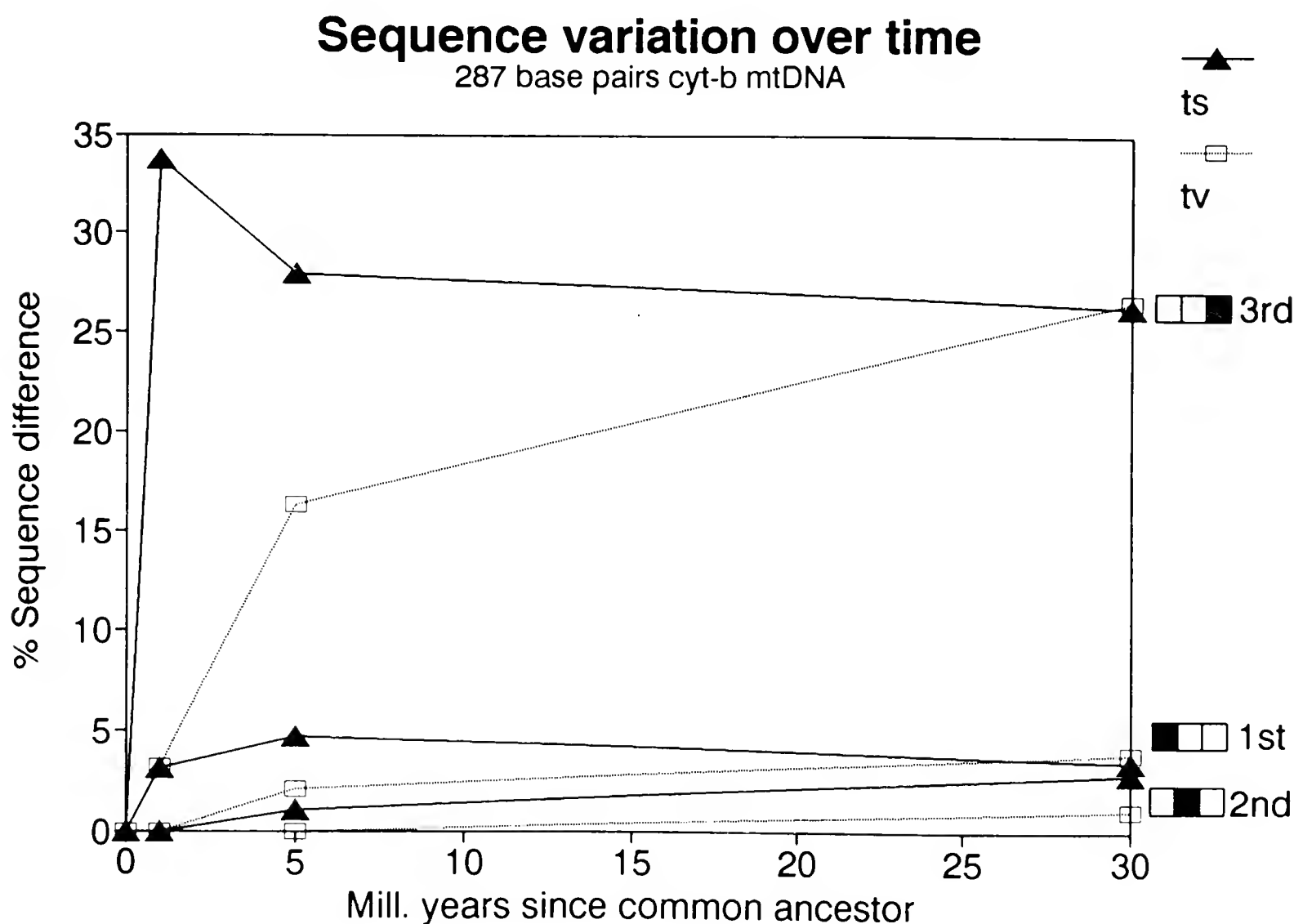


FIGURE 2 – The first 1/20 of the graph in Figure 1 in order to resolve the first 30 million years.

These relationships are illustrated in Figures 1, 2 and 3; "million years since common ancestor" refers to rough estimates based on current systematic/paleontologic views. Replacements, all 2nd position changes and transversions at 1st position, are linear functions, and the remaining curves seem to consist of three parts. At first a steep linear function occurs, exhibiting "free" evolution with no back mutations; then follows a more or less protracted curve indicating the 'multiple hit zone'; and, finally, a slowly rising linear function. The slight amplitude can be caused by slowly accumulating amino acid substitutions and evolved differences in molecular evolutionary mechanisms, because saturation phenomena alone would result in a horizontal curve. The above mentioned higher number of T's at third position in the suboscines could serve as an example of this. Third position substitutions especially exhibit an 'overshoot' of transitions in the beginning of the 'multiple hit zone' within the first 30 million years. This is due to the differences in substitution rates between transitions and transversions, where the delay in transversion substitutions postpone their inhibitory influence on transitions.

For phylogenetic analysis, these curves reveal where phylogenetic information starts to fade out. This happens extremely fast for transitions at 3rd and 1st positions (the silent leucine substitution is a transition). Transversions at 3rd position do also run into the ‘multiple hit zone’ quickly, but significantly more slowly than transitions. All transversions at 1st and 2nd positions result in replacements as do all transitions at 2nd position. At these latter positions mtDNA does not appear saturated even after 600 million years, and phylogenetic information is apparently retained. This is also the case for amino acid replacements (Figure 3). Table 2 depicts this span of variation in relation to the systematic ranks of the different bird species.

TABLE 3 – Amino acid comparison of chicken mitochondrial protein genes with mammalian and *Xenopus laevis* homologous genes (%). * For each gene, mean values are quoted for the comparison of the chicken sequence with that from all three following mammals: mouse, cow and man. Redrawn from Desjardins and Morais (1989).

Gene	Chicken/mammals*	Chicken/ <i>Xenopus</i>
ND1	70	70
ND2	45	57
COI	86	86
COII	67	70
ATPase 8	27	47
ATPase 6	55	68
COIII	75	80
ND3	57	67
ND4L	47	41
ND4	59	61
ND5	56	62
ND6	27	42
Cyt. b	74	75

Phylogenetic analysis of distantly related taxa must therefore rely mostly on replacement substitutions and transversions. The numbers of these, especially replacement substitutions, are small for cyt-b, which necessitates long stretches of sequence. Table 3 shows the relative degree of conservation for different vertebrate mitochondrial genes. Cyt-b is one of the most conservative, whereas NADH-dehydrogenase subunit 6, (ND6), is more than twice as variable and might therefore be a good choice. Although the number and rate of substitutions at 3rd position are expected to be the same as for cyt-b 2, its range of application may be larger.

There are currently significant differences in the ways we can analyze protein-coding mtDNA genes such as cyt-b and non-protein coding as the d-loop and ribosomal genes. There are fairly good hypotheses of functional domains in the d-loop sequence and of stem and loop structures of the ribosomal gene products. Patterns of conservation seem to follow this with higher degree of conservation in stems, for example (Gadaleta et al. 1989). With the growing knowledge of the pattern of variation within these parts of the mtDNA, more information can be obtained. However a problem in analyzing sequences like this is that alignment at greater evolutionary distances (e.g. between the Tyranniid families mentioned above, own unpublished results) can be ambiguous because of deletion/insertion events.

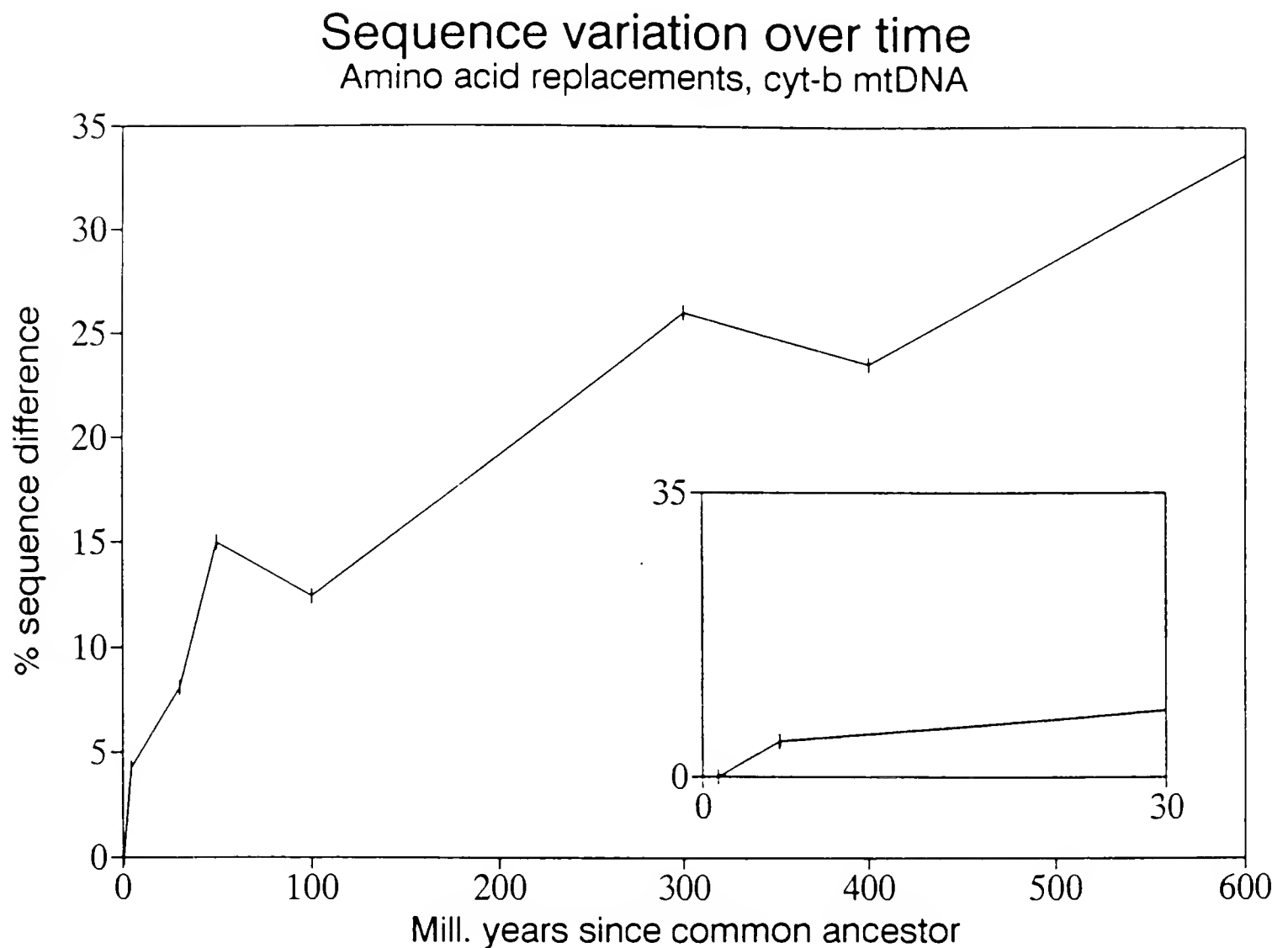


FIGURE 3 – Amino acid replacements over time. Based on the same data set as in Figure 1. Inserted is an enlargement of the first 30 million years.

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TWIGS AND BRANCHES ON THE AVIAN TREE, AS REVEALED BY DIRECT SEQUENCING OF MTDNA VIA THE POLYMERASE CHAIN REACTION

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ABSTRACT. The polymerase chain reaction (PCR) and direct sequencing are rapidly becoming the methods of choice for obtaining mitochondrial DNA sequences. Using several pairs of versatile specific primers to amplify sequences from the cytochrome b gene, we have established that in birds, as in other vertebrates, there is a fast accumulation of silent transitions and a slower accumulation of silent transversions and amino acid replacements. This range of rates has allowed us to address phylogenetic questions at several temporal levels. We shall present trees which relate (1) species within the babbler genus *Pomatostomus*, (2) these Australian babblers to Palearctic thrushes rather than to other Australian "Corvida" and (3) flamingoes to Ciconiiformes or Charadriiformes rather than to Anseriformes. The merits of this approach will be compared to that of bulk hybridization of the "single-copy" fraction of nuclear DNA, with emphasis on the notion of statistical testing.

CONCLUDING REMARKS: MODERN BIOCHEMICAL APPROACHES TO AVIAN SYSTEMATICS

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ABSTRACT. This symposium showcased modern molecular approaches to avian systematics. Gelter and Tegelstrom illustrated the use of multiple techniques in understanding the evolution of closely related species. One of the most exciting methodological developments in molecular systematics is the polymerase chain reaction (PCR), which allows easy and rapid amplification of specific sequences of DNA, which can then be easily sequenced. Johnson and Cicero, Arctander, and Edwards, Quinn and Wilson used PCR and sequencing to study mitochondrial DNA (mtDNA), which allowed them to investigate a variety of questions regarding geographic variation, speciation, phylogeny and the evolution of mtDNA itself. Baverstock and colleagues illustrated the use of immunological methods for inferring systematic relationships. Because the field of molecular evolution is large and rapidly expanding, these concluding remarks will deal not only with the contributions to this symposium, but with aspects not emphasised by the participants.

Keywords: molecular methods, mitochondrial DNA, phylogeny inference, geographic variation.

INTRODUCTION

Molecular techniques have been widely heralded in systematics because they expose genetic variation directly. Advantages of molecular methods include: the apparent uniform rate of evolution of particular genes within lineages, the existence of explicit genetic models of character evolution, the apparent selective neutrality of many molecular traits, the likelihood of genetic independence of characters, and the opportunity to evaluate homologous regions of DNA across broad taxonomic groups. Because we think of evolution ultimately in genetic terms, molecular methods are of obvious value. For instance, geographic variation has evolutionary significance if geographic patterns are genetically influenced. Speciation requires a conversion of genetic variation from within to between taxa, and a phylogeny is a genetic trace of the history of such conversion events. Thus, molecular methods provide information critical to addressing these fundamental issues.

CRITIQUE OF MOLECULAR METHODS IN AVIAN SYSTEMATICS

Hillis and Moritz (1990) summarized the value of various molecular methods for questions at different tiers in the taxonomic hierarchy. I have provided a similar set of opinions for avian systematics (Table 1). Issues considered include cost and time relative to the level and accuracy of resolution provided. Below I discuss the rationale behind my opinions.

Protein electrophoresis

I see little value in continuing protein electrophoretic studies of geographic variation in temperate-breeding birds, unless pilot studies indicate otherwise. Most studies

discovered little or no genetic differentiation despite often considerable morphological variation (Barrowclough 1983, Barrowclough & Johnson 1988). Either morphological differences are environmentally induced or the genes surveyed by protein electrophoresis do not reflect patterns of genetic differentiation underlying morphological variation. Intraspecific allozymic differentiation probably is lacking because of recency of population expansion and insufficient time for the evolution of concomitant allozyme markers. If allozyme alleles are selectively neutral (Barrowclough et al. 1985), then the substitution rate equals the mutation rate independent of effective population size in constant populations. Genetic differentiation might require a long period of time. Populations recently isolated will appear to be exchanging genes, but this is an illusion caused by retention of ancestral polymorphisms (Slatkin 1985). Thus, allozyme evolution is probably not sufficiently rapid on average to track fragmentation of temperate avian populations (Gelter & Tegelstrom, this symposium).

Protein electrophoresis does provide useful data for inference of phylogenetic relationships among congeneric species. However, with only a single data set (of any kind) one has only inferential means of ascertaining confidence in a phylogenetic estimate (e.g. Felsenstein 1985). Congruence of genetically independent data sets provides an index of a phylogeny's reliability. For example, cladograms derived from variation in allozymes and mtDNA within the genus *Ammodramus* were highly congruent, which would not be expected by chance alone (Zink & Avise 1990). The most likely factor producing such congruence is phylogeny, or common descent. Additional comparisons of mtDNA and allozymes in the genera *Zonotrichia* and *Pipilo* have indicated significant congruence (Zink et al. in press, Zink & Dittmann in press), suggesting that both types of data usually contain a discernable phylogenetic signal. At some level of divergence allozymes will provide no useful data for construction of avian phylogenies, although that limit is unknown (Lanyon & Zink 1988). Protein electrophoresis is relatively fast and inexpensive and provides information on multiple gene loci (Table 1).

TABLE 1 - Molecular techniques and levels of resolution in avian systematics. RFLP = restriction fragment length polymorphism. RAPD = randomly amplified polymorphic DNA.

Method	Geographic Variation	Pattern of Speciation	
		Recent	Ancient
Protein Electrophoresis	+/-	Yes	+/-
Nucleic Acids			
MtDNA - RFLP	Yes	Yes	+/-
MtDNA Sequences	Yes*	Yes	Yes
Nuclear RAPDs	Yes	+/-	No
Nuclear Sequences	Yes*	Yes*	Yes
Immunology	No	+/-	+/-
DNA/DNA Hybridization	No	+/-	+/-

+/- = depends on question and cost
Yes = appropriate and cost effective

No = not appropriate
Yes* = appropriate but expensive

Nucleic acids

MITOCHONDRIAL DNA. Both restriction (endonuclease) fragment length polymorphisms (RFLPs; Gelter & Tegelstrom, this symposium) and sequences (Johnson & Cicero, Arctander, and Edwards, Quinn, & Wilson; this symposium) are being used frequently in systematic studies (Moritz et al. 1987) including those dealing with birds (Shields & Helm-Bychowski 1988). Within species, mtDNA RFLPs have greater resolving power than allozymes (Awise & Zink 1988, Zink in press, Gelter and Tegelstrom this symposium), although not all species exhibit geographic differentiation. In the Fox Sparrow *Passerella iliaca* significant differences in mtDNA, morphology and breeding habitats occur at the boundary of the Sierra Nevada and Great Basin, whereas no allozyme markers were discovered (Zink in press). In many instances, mtDNA differentiation mirrors morphological breaks (Johnson & Cicero, Arctander; this symposium), but not all morphological breaks are accompanied by mtDNA differentiation. MtDNA and morphology may evolve at roughly similar rates in bird species.

A further advantage of mtDNA is the potential to construct mtDNA allele phylogenies. With allozymes, one can estimate gene frequencies, but not phylogenetic relationships among alleles segregating at individual gene loci. Alleles at a locus evolve in a hierarchical fashion, as do species in a lineage. Because one can construct a phylogenetic network of mtDNA alleles found in different geographic samples, analysis of geographic variation is facilitated (termed "phylogeography" by Awise et al. 1987).

Slatkin and Maddison (1989) show how mtDNA allele phylogenies can be used to estimate gene flow. For example, in a study (Zink et al. manuscript) of mtDNA variation within the Common Grackle *Quiscalus quiscula*, four individuals at one site each possessed a unique mtDNA clone. These four "alleles" were found nowhere else, suggesting limited gene exchange. However, phylogenetic analysis of restriction site differences revealed that the four clones did not share a most recent common clonal ancestor but rather had nearest clonal relatives in other geographic samples. Significant gene flow is indicated because clones at this locality do not trace their common ancestry to a mother that existed at that site (Slatkin & Maddison 1989).

Sequencing and RFLP analyses of mtDNA permit inference of phylogenetic relationships among avian taxa (Zink & Awise 1990; Arctander, and Edwards et al. this symposium), although I stress that mtDNA analysis provides a single "gene genealogy" embedded within the organismal phylogeny. The entire mtDNA molecule, although encoding several "genes," has a *single history* because the entire mtDNA molecule is matrilineally inherited as a single linkage group. One expects that single gene genealogies will depart from the organismal phylogeny (Pamilo & Nei 1988), especially in the interval of $4N$ (N = population size) generations after the nuclear gene pools become isolated (Neigel & Awise 1986, Ball et al. 1990). Comparison of mtDNA-based cladograms with those derived from other character sets are necessary to measure confidence that any mtDNA tree (even if the entire molecule has been sequenced) reflects the organismal tree.

NUCLEAR GENES. To complement mtDNA analyses, a pressing need is for similar studies (especially sequencing) of nuclear genes. At this point, few have attempted sequencing or RFLP studies in avian systematics (Mindell & Honeycutt 1989, Gelter & Tegelstrom this symposium). The amplification of nuclear DNA using random

primers offers the exciting potential to detect genetic markers for use in intraspecific studies (Williams et al. in press).

ANALYZING NUCLEIC ACIDS. Sequence comparisons will become one if not the major tool of molecular systematists, as revealed in this symposium. Although DNA sequencing is of interest at all levels, it is sometimes too expensive (at present) relative to other methods that can answer the same question. Also, with only four bases possible, nucleotide positions become "saturated" with base substitutions, and beyond a certain level of divergence some sequences are uninformative because multiple substitution events at a position cannot be discovered. Insertions and deletions in DNA, recognized as "gaps" in sequence alignments, are frequent phenomena that present serious analytical problems (Felsenstein 1988). Nonetheless, comparison of DNA sequences represents the major advance in systematics.

Immunology and DNA-DNA Hybridization

These (distance) techniques are those that produce a single measure of similarity or difference between pairs of taxa. Immunological techniques, addressed in this symposium by Baverstock and colleagues, produce interesting information. These techniques probably are not appropriate for phylogeny inference (Table 1; Baverstock et al. this symposium) because they suffer several biases such as non-reciprocity. Furthermore, immunological techniques measure genetic differentiation at a single locus, and as discussed above, single genes might often be discordant with organismal phylogenies (Pamilo & Nei 1988). Immunological distance values can be mapped onto a phylogeny to reveal differences in evolutionary rates. However, there are too many reasons why a distance tree can be incorrect for them to be primary tools for phylogeny inference, and these reasons are difficult to study when all data are combined into a single distance measure (Swofford & Olsen 1990). DNA-DNA hybridization is also a secondary tool for phylogeny inference because of the many correction factors that are required for the technique to yield reliable phylogenies (Werman et al. 1990; see Krajewski [1989] for another opinion), except perhaps for anciently diverged taxa (Table 1), where sequence comparisons are compromised by insertions and deletions. It would be of comparatively greater interest to map DNA-DNA hybridization values onto a phylogeny than those derived from immunological (single gene) comparisons because the former surveys many genes.

Techniques versus questions

Although the phenomena investigated by systematists are inherently genetical, molecular methods are not a panacea. Many have assumed that having genetic information superseded attention to data analysis and to evolutionary questions themselves. Some aspects of the evolutionary process will be difficult to resolve with molecular (or any) techniques. Some speciation patterns, those with closely spaced nodes occurring a relatively long time ago, cannot be discerned with characters that evolve at constant rates (Lanyon 1988). Thus, what was heralded as the virtue of molecular characters, their uniform rate of change, insures that they will be unable to resolve certain types of phylogenetic patterns. Characters involved in "key innovations" might be required to document monophyly of lineages that diverged close in time - such characters might be morphological or biochemical (e.g. protein or RNA configurations). Although it was once thought that molecular methods would expose the "genetics of speciation" it is now realized that unless one can study directly the genes that influence ranking traits (those that delimit species boundaries) we will still only

have indirect knowledge of processes of speciation (Cracraft 1989, Zink in press). Consequently, molecular characters will not be the data of choice for all questions in systematics and evolutionary biology. Nonetheless, a powerful and growing battery of molecular techniques permits robust inferences of evolutionary patterns and processes.

RATES OF MOLECULAR EVOLUTION

A reason for early enthusiasm about molecular methods was the postulated existence of a molecular clock. Ensuing years have indicated that rate constancy is likely limited to clades and molecules (Vawter & Brown 1986). Attempts to calibrate multi-locus allozyme clocks reached little agreement (Avice & Aquadro 1982). The one attempt to calibrate an avian molecular clock (Gutierrez et al. 1983) was based upon a fragment of quail skeleton. This fossil was taken as the minimum age of a particular lineage and led to the suggestion that one unit of Nei's (1978) genetic distance accrued in 26.3 million years. Marten and Johnson (1986) challenged this fossil's dating and suggested a calibration of 19.7 million years. Clearly, a calibration based on one data point is dubious at best. Calibration of mtDNA evolution in birds, namely 2% sequence divergence per million years, agrees with the value estimated for primates (Shields & Wilson 1987). Opportunities to calibrate molecular divergences among avian taxa are limited by lack of information on relevant fossils.

With inadequate information, one is left with indirect means of estimating confidence in calibration factors. I compared estimates of divergence dates for several avian taxa using allozyme and mtDNA data. On average, plots of allozyme and mtDNA estimates of differentiation should yield a slope of 1.0 if the two are equally good at measuring evolutionary separation (indeed, if they are not, then even an "approximate" clock does not exist). This does not address the reliability of the calibrations based on quail and goose fossil remains. If the two independent calibrations gave the same divergence date for pairs of taxa, the slope should not only be one, but the regression line should pass through the origin.

I plotted mtDNA (RFLP) and allozyme estimates of dates of divergence for shorebirds (Dittmann & Zink, unpubl. data), towhees (Zink & Dittmann in press) and sparrows (Kessler & Avice 1985, Zink et al. in press). Using the calibration for allozymes of 26.3, the y-intercept was 0.37 and the slope was 1.44. The calibration of 19.7 (Figure 1) yields a slope of nearly 1.0 and a y-intercept of 0.27; 65% of the variance is explained. Although there is an apparent saturation effect in the mtDNA data (due mostly to the shorebird data), these two independent estimates provide very similar estimates of divergence dates, warranting further study.

ARE MOLECULAR METHODS BETTER THAN MORPHOLOGICAL ONES FOR INFERENCE OF PHYLOGENIES?

The literature has seen numerous debates on molecules versus morphology. Hillis (1987) noted that this is an unfortunate contrast, as most dichotomies usually are. For study of geographic variation and speciation, I consider molecular methods necessary for a study to be complete. In phylogeny inference, however, the roles of

morphological and molecular data are unclear. There are differences in the nature and analysis of molecular and morphological data. For example, morphologists study variation in their taxa and define characters a priori, which can mitigate the effect of homoplasy and invariant characters. Molecular systematists choose a region of the genome, which is a deliberate rather than a random choice, but then the characters (e.g., bases in a DNA sequence) are evaluated without prejudice. In the analysis of molecular data the number of character states is often limited, whereas there may be many states in a morphological character (Mickey & Weller 1990). Also, morphological characters likely have significant genetic covariation, yet they are analyzed as though genetically independent, whereas molecular characters, if from unlinked genes, are likely independent in genetic transmission. In my opinion, a molecular method is the method of choice if the broad limits of the group are already known (probably based on morphology!), multiple genes can be sequenced, these genes exhibit appropriate rates of evolution, and the evolutionary history of the group in question does not consist of closely spaced ancient nodes. Even then, if the phylogenetic estimate does not strongly favor one particular branching structure, one should not be overconfident in the pattern. Similarly, one should not be overconfident in a gene tree (e.g., mtDNA gene lineage) no matter how robust it is, because it simply might not reflect the species tree (Pamilo & Nei 1988, Nei 1987).

Many might feel that molecular methods are inherently superior for phylogeny inference because they expose genetic variation directly. Comparisons of independent

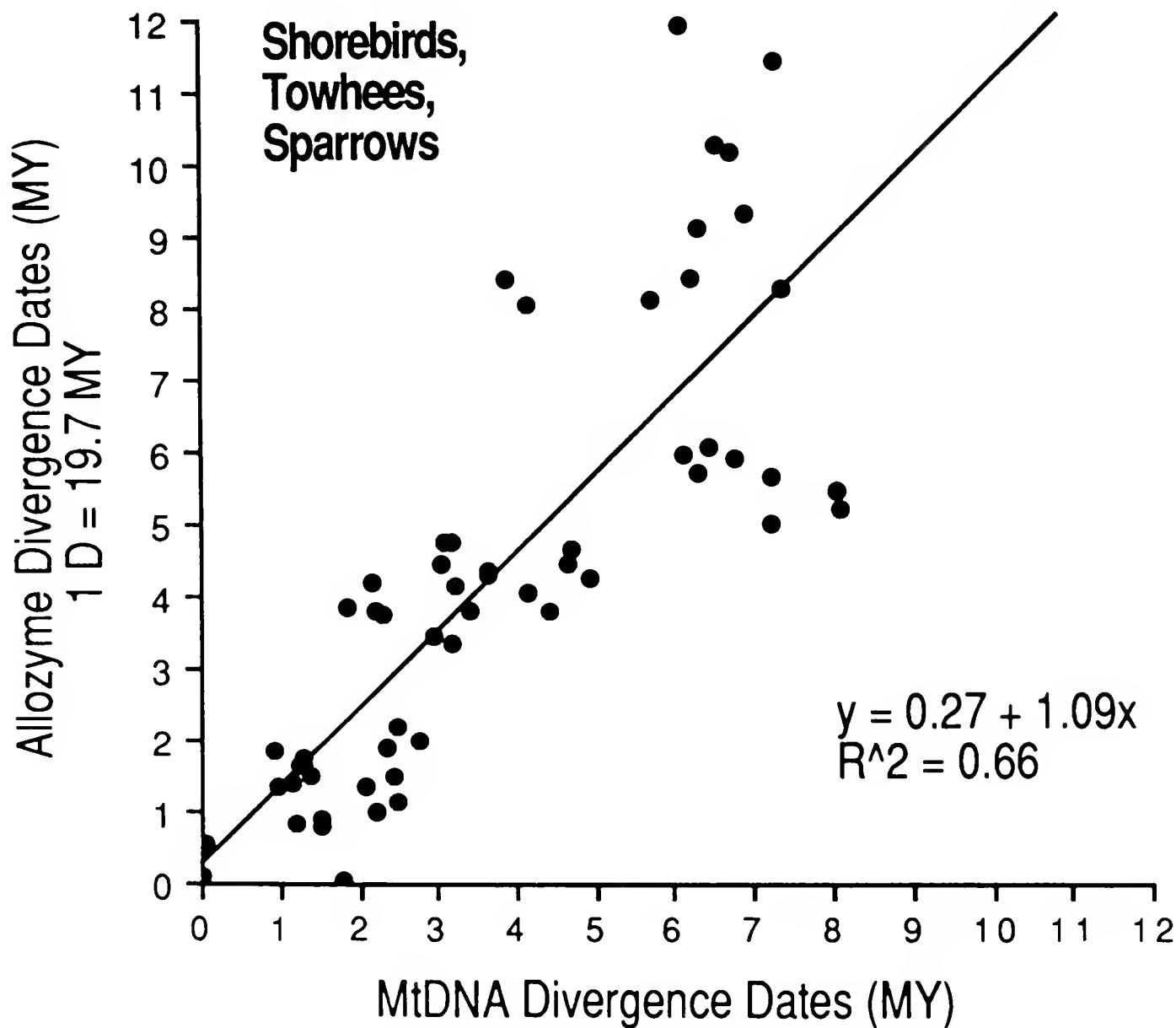


FIGURE 1 - Plot of mtDNA versus allozyme dates of divergence for towhees (*Pipilo*), sparrows (*Zonotrichia*, *Junco*, *Melospiza*), and shorebirds (*Phalaropus*, *Calidris*, *Tringa*, *Limnodromus*, *Recurvirostra*).

molecular estimates of the same sets of taxa will establish the robustness and levels of homoplasy in molecular data sets (the same is true for morphology). If multiple molecular data sets support a robust phylogeny, morphological data sets can be examined to determine their reliability for phylogeny inference in that group. We can anticipate several outcomes. First, the problems with analysis of molecular data might be too great for them to be consistently "superior." Second, it might prove that morphological data sets are best mapped onto a phylogeny derived from molecular data sets, thus revealing the nature of morphological evolution in particular lineages. Third, morphology might prove equally efficient (and cheaper) at recovering information about hierarchical relations among organisms. Fourth, morphology and molecules might be equally ambiguous, indicating that the nature of the evolutionary history is recalcitrant to its recovery (Lanyon 1988). It is not yet apparent which of these outcomes is most consistent in general with the results of evolution. Multiple data sets are complementary and are needed for a complete understanding of evolutionary patterns and processes.

CONCLUSIONS

Many aspects of avian systematics have proved difficult to understand when studied by traditional methods, and the field of avian systematics has for the most part languished during the past 30-40 years. Molecular methods have infused new enthusiasm into the field that is demonstrated in this symposium. The future will, I think, yield important insights into avian population structure and evolutionary processes, and the phylogenetic relationships of many avian groups. Systematics is indeed alive and well, and should be an increasingly important field of study for ornithologists.

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